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The specialized white-sand flora of the Uatumã Sustainable Development Reserve, central Amazon, Brazil

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Abstract

The consensus is that Amazonian white-sand ecosystems (campinaranas) shelter several endemic plant species. However, recent studies have shown that most species are generalists, and they also occur in other Neotropical ecosystems. To investigate this issue, we analyzed the proportion of endemic/specialist species in a checklist of trees, palms, and shrubs sampled between 2014 and 2020 in campinarana patches of the Uatumã Sustainable Development Reserve (USDR), central Amazon. We also provide a description of phytophysiognomies, habitats, distribution, and phenology. We found 167 species belonging to 117 genera and 50 families. Fabaceae was the most representative (21 spp.), followed by Rubiaceae (16 spp.) and Chrysobalanaceae (10 spp.). We found that 30.5% of the species were exclusive to campinaranas, confirming that although there are many endemics, proportionally most species are generalists. The USDR has a rich flora specialized in oligotrophic habitats, which must be considered in the management and conservation strategies of these complex and fragile Amazonian ecosystems.

Keywords

Amazonian flora, biodiversity, campinarana, endemic flora, floristic, oligotrophic environment, wetland conservation

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Introduction

The Amazon, the biome with the greatest biodiversity worldwide, is formed by a mosaic of ecosystems with various floristic compositions, vegetation structure, and diversity patterns (Antonelli et al. 2018; Tuomisto et al. 2019). The largest extension of the Amazon basin is covered by tall and exuberant upland forests (terra-firme) and floodplain forests (igapó and várzea) along the large rivers. However, relatively few scientific studies have addressed the other vegetation formations that are fragmented and interspersed in the Amazon landscape. This is the case of the oligotrophic plant formations on sandy, nutrient-poor, acidic, and highly leached soils (Luizão et al. 2007; Mendonça et al. 2015), known by various names, such as white-sand vegetation, campina, campinarana, wallaba, varilal, bana, muri or caatinga-amazonica. Here, we will follow the habitat nomenclature as suggested by Veloso et al. (1991) and IBGE (2012), and use the term campinarana.

The campinarana is not homogeneously distributed across the Amazon basin. While in the upper Negro basin it is the predominant formation covering large and continuous areas, in most of the Amazon basin it is fragmented, interspersed as small "islands" of differentiated vegetation surrounded by a matrix of terra-firme forests (Anderson 1981; Prance 1996). Estimates indicate that this type of vegetation covers 334,879 km^2, equivalent to about 5% of the area of the Amazon basin (Adeney et al. 2016). Campinaranas can have different geological origins and genesis. In some areas, the podzolization process acts in the impoverishment of lateritic soils, with the leaching promoting a gradual loss of the clay fraction, leaving primarily the sand fraction which gives the soil greater porosity and favors the migration of organic matter (Klinge 1965; Mendonça et al. 2015). Other areas originate from the weathering of sandy rocks, such as sandstones (Rossetti et al. 2012), or from reworking sediments originating from paleochannels or paleodunes of the Pleistocene–Holocene (Rossetti et al. 2012, 2019).

These formations can present various phytophysiognomies and floristic compositions throughout their area of occurrence, varying from open grasslands to savanna-like formations dominated by shrubs and treelets, to stratified forests with emerging trees reaching heights of up to 25 m (Veloso et al. 1991; IBGE 2012; Adeney et al. 2016). The variation in species composition, structure, and diversity is mainly related to differences in the water table and soil texture, as well as nutritional changes in soils (Tiessen et al. 1994; Coomes and Grubb 1996; Coomes 1997; Damasco et al. 2013; Targhetta et al. 2015; Demarchi et al. 2018). However, other factors such as the geological origin (Rossetti et al. 2019), fire (Adeney et al. 2009), and pre-Columbian and recent anthropic disturbances (Prance and Schubart 1977; Ferreira et al. 2013; McMichael 2021) can also play an important role.

During the course of a year, the plant community of campinarana may experience two opposite environmental stressors: drought and flooding. The intense leaching of sandy soils reallocates and deposits Fe, Al, Mg, and other compounds in the lower layers of the soil. This process forms a cemented layer (hardpan) that can block water drainage and, thus, during the wet season, excessive rainfall subjects some physiognomies to the (shallow) flooding or waterlogging of the root system through elevated groundwater levels for months (Richardt et al. 1975; Kubitzki 1989; Quesada et al. 2011); therefore, many campinaranas are classified as wetlands (Junk et al. 2011). In contrast, during the dry season, the low water retention capacity of sandy soils, combined with high temperatures and related high evapotranspiration rates, lead plants to suffer from physiological drought (Franco and Dezzeo 1994). This results in the structure of vegetation similar to savannas, which in this case is not induced by climate conditions (as annual rainfall exceeds in most locations of campinaranas 2000 mm; Adeney et al. 2016), but related to the edaphic conditions. These environmental factors may function as environmental filters for many plant species, requiring species-specific adaptations to occupy and reproduce in this habitat, resulting in a specialized flora with several endemic taxa (Anderson 1981; Boubli 2002; Fine et al. 2010; Adeney et al. 2016; Fine and Baraloto 2016; Guevara et al. 2016).

Most studies carried out with biological groups in campinaranas point to a high number of specialized and endemic species, such as plants (Anderson 1981; Fine and Baraloto 2016; Guevara et al. 2016; Costa et al. 2020) and birds (Borges et al. 2016). In fact, several plant species and genera endemic to these ecosystems are known, but there are also analyses suggesting that the vast majority of campinarana species are generalists, occurring in a range of other Amazonian and non-Amazonian ecosystems (García-Villacorta et al. 2016). In a large-scale analysis using up to 1,500 floristic plots distributed throughout the Amazon, ter Steege et al. (2013) showed that half of all trees in campinaranas belong to only 25 species, 15 of which also hyperdominant in other Amazonian ecosystems. Therefore, the proportion of specialized and endemic tree species in Amazonian campinaranas is still a matter of debate. The lack of robust trends in the available data is linked to the fact that almost all campinarana inventories are concentrated in few areas, usually close to cities and research centers, while large sampling gaps exist in many remote locations (Hopkins 2007).

Nowadays, estimations on the total number of tree species in the Amazon basin range between 12,500 and 15,000 tree species (with diameter at ground height – DBH ≥10 cm) (Hubbell et al. 2008; ter Steege et al. 2013, 2020), but only 6,727 tree species are known to science so far (Cardoso et al. 2017). Although current estimates can be questioned due to differing methodologies and the lack of taxonomic precision of the available databases derived from plot inventories (see discussion by Cardoso et al. 2017), the Amazon has immense areas that

remain poorly sampled (Hopkins 2007, 2019). Many species, especially those with a small geographic range are still to be recorded or described, including trees, shrubs, vines, epiphytes, and terrestrial herbs.

Floristic studies in areas that are difficult to access with low sampling effort are crucial to fill the gaps of knowledge about the Amazonian flora. In addition, these studies provide important taxonomic and biogeographic information for supporting management strategies and for the definition of protected areas, as detailed floristic inventories often find new populations of endangered and little-known species (Keller et al. 2021). In this study, we make use of floristic inventories and surveys of campinaranas during the last seven years in the Uatumã Sustainable Development Reserve (USDR), combined with environmental parameter data, to describe physiognomies of the campinaranas. Further, we compare our species list to collections deposited in herbaria and other inventories in order to classify species as white-sand specialists, endemics, or generalists as a contribution to the knowledge of the campinarana flora and subsidize conservation strategies for these ecosystems.

Study Area

The USDR is a protected area which aims to reconcile the conservation of biodiversity and the subsistence of the resident human population. The area covers about 4,244 km² and is located in the northeast of the Amazonas state, Brazil, in the municipalities of Itapiranga and São Sebastião do Uatumã (Fig. 1). The Uatumã River drains the USDR along its entire length, in addition to other important tributaries such as the Abacate and Jatapú. All rivers in the region are sediment- and nutrient-poor black-water rivers (Junk et al. 2015; Lopes et al. 2019).

The climate is equatorial pluvial (Radam Brasil 1978) with remarkable seasonality in precipitation and an annual average of 2,077 ± 438.3 mm (analyzed period of 1975–2005); the rainy season lasts from December to May, with a peak in March and April (monthly average of 298.4 and 278.7 mm, respectively) (Carneiro and Trancoso 2007). The dry season lasts from June to October, with August and September being driest (monthly average of 72 mm). The annual average temperature is 27 °C (Carneiro and Trancoso 2007), and locally can reach a high amplitude, for example, in the open shrubby campinarana temperatures can reach up to 48 °C during the day and drop to more than 20 °C overnight (LOD unpublished data).

The USDR is mostly covered by upland forests (terra-firme or Lowland Dense Ombrophilous Forest according to IBGE 2012); the banks along the large black-water rivers subject to floods are covered by floodplain forests (igapó). The campinarana formations occur on ancient river terraces located between the current river terraces (Uatumã River) and the plateau slopes, where the terra-firme forest predominantly occurs. The campinaranas are scattered in the middle of a matrix of terra-firme forests, as small patches of differentiated vegetation. The patches occupy an area of 34,800 ha which is equivalent to about 8% of the USDR (Fig. 1). The majority of campinaranas in the USDR are integrated into the zone of strict biodiversity protection, while smaller areas are located within the zone for extensive land use (extraction of timber and non-timber forest products) (Schöngart et al. 2021).

Methods

Phytophysiognomies. Based on our field observations, systematic botanical collections (see details below), environmental parameter data, and previous studies (Targhetta et al. 2015), we describe the campinarana phytophysiognomies that occur in the USDR, highlighting the representative species of each category. This categorization is based mainly on vegetation structure (height, density, and basal area), floristic composition, and variation of the groundwater table throughout the year. The data used to contextualize the descriptions of the phytophysiognomies are from the present study and from the permanent plots of the PELD-MAUA project (Long Term Ecological Research Network - Ecology, Monitoring and Sustainable Use of Wetlands; detailed info can be accessed at https://peld-maua.inpa.gov.br/). The campinarana phytophysiognomies are also in accordance with the classification of vegetation types proposed by Veloso et al. (1991) and IBGE (2012).

Floristic survey. Field activities were conducted in several excursions between 2014 and 2017, and monthly from March 2018 to March 2020; therefore, it was possible to collect fertile samples from almost all recorded species. For species sampling, we followed the method proposed by Filgueiras et al. (1994), where pre-existing trails outside the plots were used to collect all species (shrubs, treelets, and trees) found. We also used six plots, each with an area of 50 × 50 m previously installed in 2013 in forest phytophysiognomies by the PELD-MAUA project (sampling criteria: diameter at breast height (DBH) ≥ 10 cm) and other six plots, each with an area of 50 × 50 m installed in 2017 in non-forest phytophysiognomies (sampling criteria: diameter at ground height (DGH) ≥ 5 cm) where all individuals sampled according to the inclusion criteria and randomly found in the plots were recorded. Fertile samples were collected, herborized, and incorporated into the INPA and EAFM herbaria (acronyms follow Thiers 2021).

Specimens were identified by comparison with exsiccata deposited in the INPA herbaria, consultation of digital images from virtual herbaria (Herbário Virtual Reflora (2021), SpeciesLink (2021), Jabot (JBRJ 2021) and Field Museum (2021)), consultation of specialized literature of each group and expert taxonomists in some specific groups. Exsiccata collected by other researchers in the USDR were verified and included in the list. We

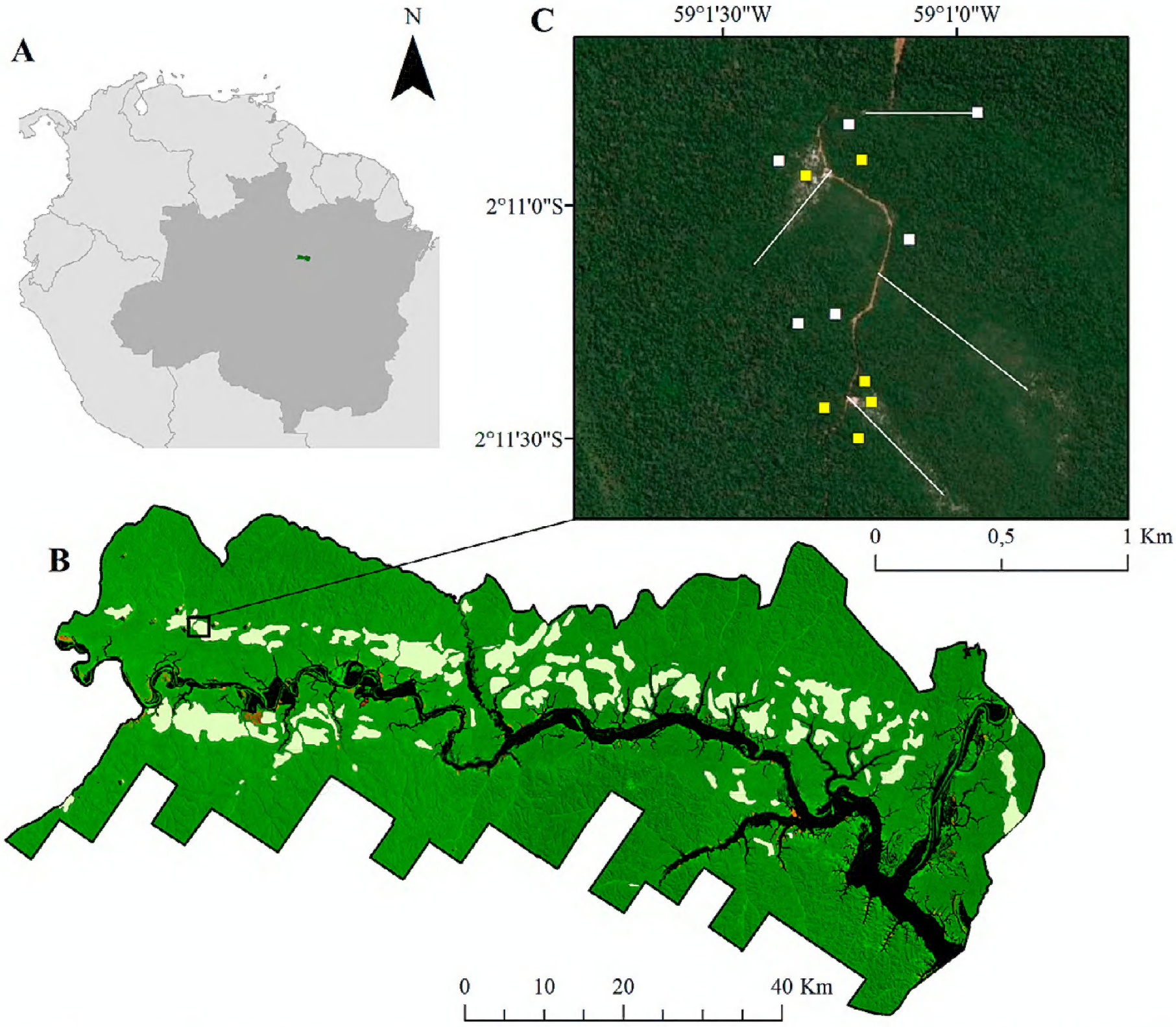

Figure 1. A. Geographic location of study area (small green area in the center of the figure), within South America. Dark gray highlights the Brazilian Amazon. **B.** Boundaries of the Uatumã Sustainable Development Reserve, with the campinarana patches highlighted in white; we delimited the campinarana patches through the manual classification of LANDSAT satellite images. **C.** Allocation of plots and sampling trails within a campinarana patches sampled, surrounded by a matrix of upland forest (terra-firme). The white squares represent plots installed in 2013 by the PELD-MAUA project, the yellow squares represent plots installed in 2017 in the context of this study.

excluded all species with dubious taxonomic identification. Species names and synonyms follow the Flora do Brasil (2021).

In order to investigate the pattern of endemic/specialist species in the campinaranas of USDR, we first gathered information about species distribution. This data within Brazil was estimated according to the information available in the database of the Flora do Brasil (2021) and integrated herbaria network SpeciesLink (2021); we included only SpeciesLink records where digital images were available and identifications were performed by taxonomic experts. The distribution of species outside Brazil were estimated according to Tropicos.org (2021), Plants of the World (2021), and Global Biodiversity Information Facility (2021). Species were classified as follows: Neotropical (neo) = species distributed to tropical and/or subtropical regions of the Americas; South America (sam) = species distributed to tropical and/or subtropical regions of South America; Amazon basin (amz) = species with occurrence restricted to the Amazon basin; Brazilian Amazon (bam) = species with occurrence restricted to the Brazilian Amazon basin.

Within the Amazonian distribution, we classified species according to their occurrence in the Amazonian forest formations (habitat), proposing three categories: 1) generalist (gen) = species with occurrence in campinarana, and any other habitats of the Neotropical region, such as upland forests (terra-firme), coastal white-sand forests (restinga), black-water floodplain forests (igapó), white-water floodplain forests (várzea), swamp forests (baixio), montane forests, savannas, among others; 2) oligotrophic habitat specialist (ohs) = species that occur in oligotrophic habitats (campinarana, restinga and igapó habitats); 3) white-sand specialist (wss): species that occur exclusively in campinarana habitats (i.e., endemics of campinaranas). For the classification of species within these categories, we used the occurrence habitats available on the labels of the exsiccata (e.g. campina, campinarana, campo de areia, savanna on the sand, varillales, bana, caatinga amazônica, among others) deposited

in the INPA herbaria and other herbaria samples from virtual herbaria. We excluded records in which exsiccata labels did not have a habitat description or raised doubts. This data cleaning caused an average of 40–60% of herbaria samples discarded by species, but made the analyzed record set more reliable and replicable for our purposes. We also consulted taxonomic studies that provided information about species' preferred habitats and the habitat information available at Flora do Brasil (2021). If varieties or subspecies were known, we considered these for the analysis of species distribution and habitat preferences.

Results

Phytophysiognomies. We classified the campinarana of USDR into six phytophysiognomies (Figs. 2, 3) as described below:

Open shrubby campinarana (OSC): composed mainly of branched shrubs, sparse small trees (DBH 5–10 cm), and many thin treelets (DGH ≤ 5 cm), forming islands of vegetation in open areas with exposed soil. The canopy of treelets reaches 2–4 m height. The soil has a little organic matter and consequently low moisture retention capacity; the deep groundwater table does not reach the surface. The exposed white sand heats up to high temperatures (above 40 °C), requiring a community with adaptations to extremely dry conditions. In the exposed sandy soil areas, there is a prominent herbaceous component, dominated by Convolvulaceae, Cyperaceae, and Orchidaceae. Some tree species with heights of up to 4 m, such as *Aldina heterophylla* Spruce ex Benth. (Fabaceae) and shrub species, such as *Humiria balsamifera* Aubl. (Humiriaceae), function as umbrella species by providing shade and consequently favoring the establishment of more shade-tolerant species. The treelets and shrubs that dominate are *Bredemeyera myrtifolia* (A.W.Benn.) Marques (Polygalaceae), *Coccoloba parimensis* Benth. (Polygonaceae), *Cybianthus fulvopulverulentus* (Mez) G.Agostini (Primulaceae), *Macrolobium punctatum* Spruce ex Benth. (Fabaceae), and *Myrcia citrifolia* (Aubl.) Urb. (Myrtaceae) (Figs. 2A, 3A).

Dense shrubby campinarana (DSC): composed of branched shrubs and thin treelets (DGH ≤ 5 cm) that form dense, almost impenetrable stands. The canopy reaches 2–5 m height, with some emerging individuals of the palm species *Mauritia carana* Wallace (Arecaceae) that reaches up to 8 m. During the wet season,

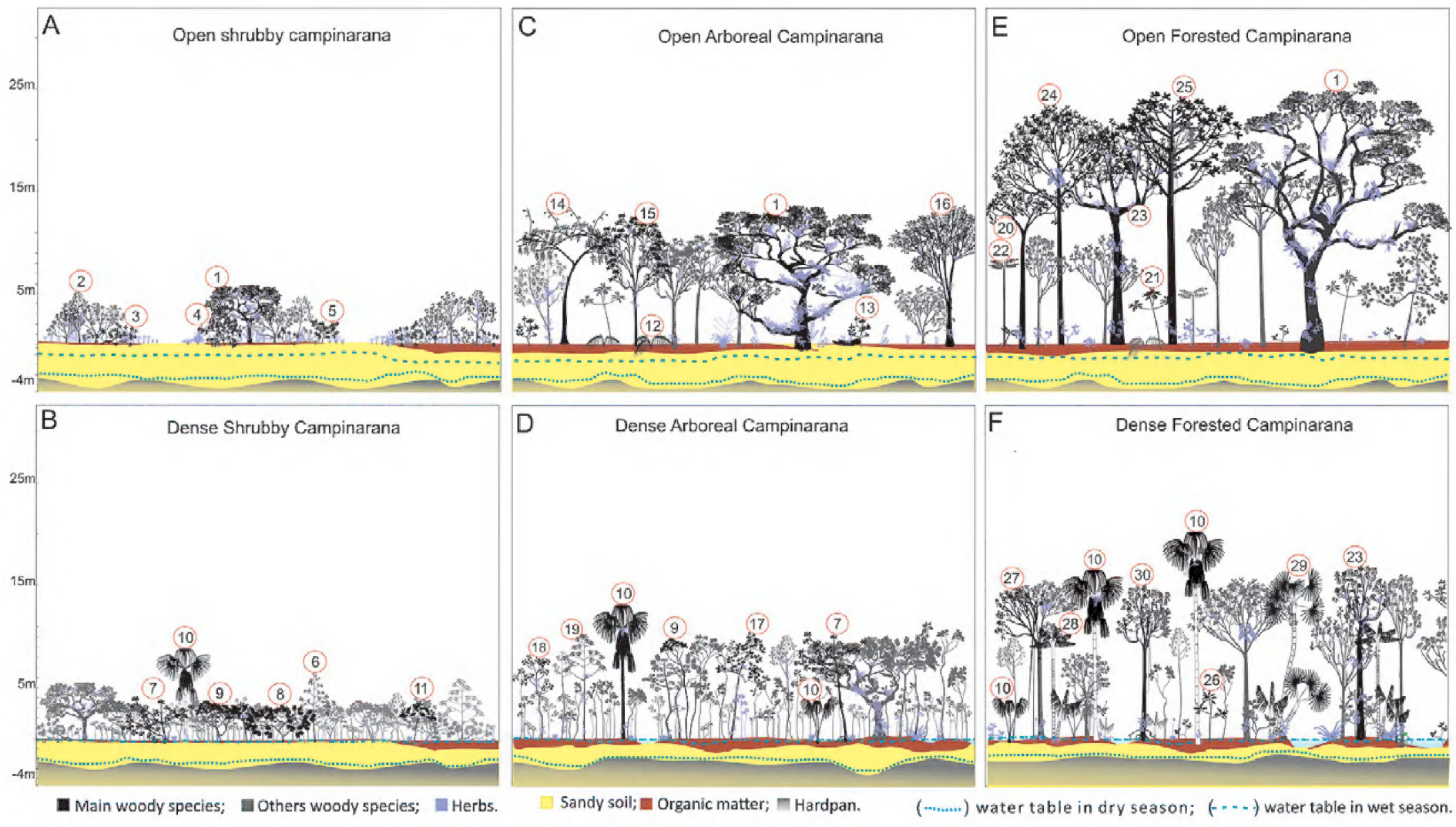

Figure 2. Schematic representation of the campinarana phytophysiognomies from Uatumã Sustainable Development Reserve, the main representative species of each one and its numbering relative to the figure. **A.** Open shrubby campinarana (OSC), (1) *Aldina heterophylla* (Fabaceae), (2) *Cybianthus fulvopulverulentus* (Primulaceae), (3) *Humiria balsamifera* (Humiriaceae), (4) *Macrolobium punctatum* (Fabaceae), (5) *Myrcia citrifolia* (Myrtaceae). **B.** Dense shrubby campinarana (DSC), (6) *Chaunochiton angustifolium* (Aptandraceae), (7) *Clusia nemorosa* (Clusiaceae), (8) *Dimorphandra campinarum* (Fabaceae), (9) *Macairea theresiae* (Melastomataceae), (10) *Mauritia carana* (Arecaceae), (11) *Remijia morilloi* (Rubiaceae). **C.** Open arboreal campinarana (OAC), (12) *Attalea microcarpa* (Arecaceae), (13) *Miconia subsimplex* (Melastomataceae), (14) *Parkia igneiflora* (Fabaceae), (15) *Pradosia schomburgkiana* (Sapotaceae), (16) *Simaba guianensis* (Simaroubaceae). **D.** Dense arboreal campinarana (DAC), (17) *Emmotum orbiculatum* (Metteniusaceae), (18) *Ilex divaricata* (Aquifoliaceae), (19) *Pagamea coriacea* (Rubiaceae). **E.** Open forested campinarana (OFC), (20) *Catostemma sclerophyllum* (Malvaceae), (21) *Duroia saccifera* (Rubiaceae), (22) *Iriartella setigera* (Arecaceae), (23) *Manilkara bidentata* (Sapotaceae), (24) *Sacoglottis mattogrossensis* (Humiriaceae), (25) *Sterigmapetalum plumbeum* (Rhizophoraceae). **F.** Dense forested campinarana (DFC), (26) *Adiscanthus fusciflorus* (Rutaceae), (27) *Clusia insignis* (Clusiaceae), (28) *Euterpe catinga* (Arecaceae), (29) *Mauritiella armata* (Arecaceae), (30) *Tovomita calophyllophylla* (Clusiaceae).

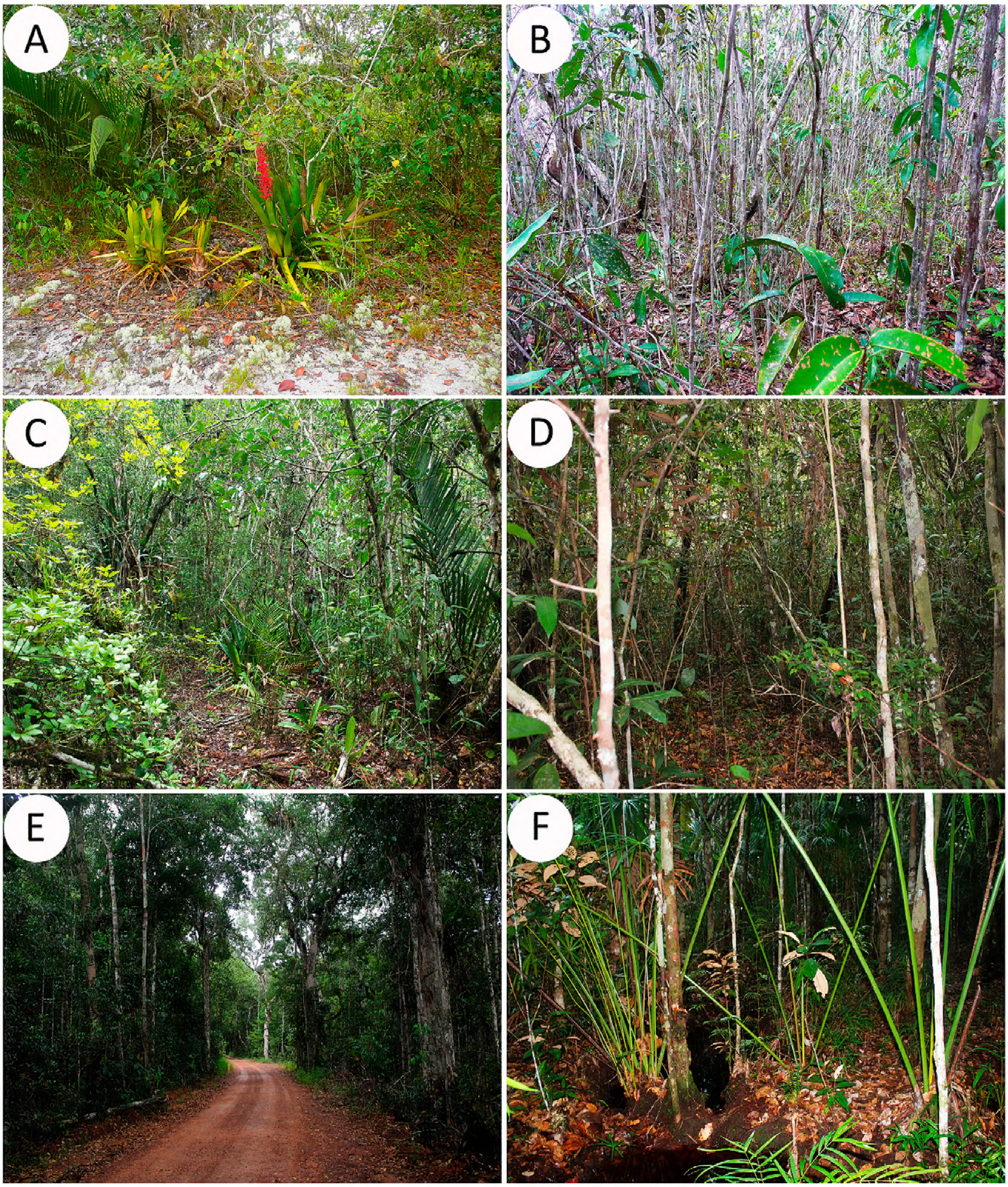

Figure 3. Phytophysiognomies from campinaranas of Uatumã Sustainable Development Reserve. **A.** Open shrubby campinarana (OSC). **B.** Dense shrubby campinarana (DSC). **C.** Open arboreal campinarana (OAC). **D.** Dense arboreal campinarana (DAC). **E.** Open forested campinarana (OFC). **F.** Dense forested campinarana (DFC).

the groundwater table reaches the surface, which results in inundation and waterlogging of the root system, and favors the colonization of annual herbs of the families Eriocaulaceae, Lentibulariaceae, and Xyridaceae. Dominant treelets and shrubs are *Chaunochiton angustifolium* Sleumer (Aptandraceae), *Clusia nemorosa* G. Mey. (Clusiaceae), *Dimorphandra campinarum* Ducke (Fabaceae), *Elaeoluma schomburgkiana* (Miq.) Baill. (Sapotaceae), *Macairea theresiae* Cogn. (Melastomataceae), and *Remijia morilloi* Steyerm. (Rubiaceae) (Figs, 2B, 3B).

Open arboreal campinarana (OAC): characteristic of the transition between open shrubby and open forested physiognomies, mainly composed of more widely spaced trees and treelets, with an open understory of easy locomotion. The canopy reaches 5–12 m height and does not show visible stratification. The soil is usually entirely covered and presents a higher amount of litter than the shrubby campinarana, allowing for higher

moisture retention. Few emergent individuals of *Aldina heterophylla* may reach relatively large basal areas (DBH ≥ 50 cm) and usually host a pronounced epiphytic component, with several species of Araceae, Bromeliaceae, and Orchidaceae. Dominant trees, palms, and treelets are *Attalea microcarpa* Mart. (Arecaceae), *Cybianthus fulvopulverulentus*, *Licania hypoleuca* Benth. (Chrysobalanaceae), *Miconia subsimplex* Pilg. (Melastomataceae), *Neea obovata* Spruce ex Heimerl (Nyctaginaceae), *Parkia igneiflora* Ducke (Fabaceae), *Pradosia schomburgkiana* (A.DC.) Cronquist (Sapotaceae), and *Simaba guianensis* Aubl. (Simaroubaceae) (Figs. 2C, 3C).

Dense arboreal campinarana (DAC): represents the ecotone between dense shrubby and dense forested campinaranas, being composed mainly of few larger trees (DBH ≥ 30 cm) and many treelets (DGH ≤ 5 cm) reaching high densities, impairing the movement. The canopy height ranges between 5 and 10 m, with low stratification. This characteristic prevents light penetration to the soil, resulting in a scarcely developed herbaceous layer. The groundwater table reaches the surface during the wet season, leading to shallow inundation of the root system for periods of up to several months. The most frequent trees, palms, and treelets are *Clusia nemorosa*, *Emmotum orbiculatum* (Benth.) Miers (Metteniusaceae), *Ilex divaricata* Mart. ex Reissek (Aquifoliaceae), *Macairea theresiae*, *Mauritia carana*, *Pagamea coriacea* Spruce ex Benth. (Rubiaceae), and *Protium heptaphyllum* subsp. *ulei* (Swart) Daly (Burseraceae) (Figs. 2D, 3D).

Open forested campinarana (OFC): forest with pronounced stratification, continuous canopy cover, open understory facilitating the movement, and with the highest species richness compared to the other physiognomies. It accumulates a large amount of leaf litter along with a thick layer of fine absorption roots. The groundwater table does not reach the surface. The canopy height ranges between 12 and 20 m, with some emerging individuals of *Aldina heterophylla* and *Sterigmapetalum plumbeum* Aymard & Cuello (Rhizophoraceae) reaching heights of up to 25 m. Frequent canopy trees are *Catostemma sclerophyllum* Ducke (Malvaceae), *Chrysophyllum sanguinolentum* subsp. *balata* (Ducke) T.D.Penn. (Sapotaceae), *Hymenopus reticulatus* (Prance) Sothers & Prance (Chrysobalanaceae), *Manilkara bidentata* (A.DC.) A.Chev. (Sapotaceae), and *Sacoglottis mattogrossensis* Malme (Humiriaceae). The most frequent understory tree species are *Dulacia candida* (Poepp.) Kuntze (Olacaceae), *Duroia saccifera* (Schult. & Schult.f.) K.Schum. (Rubiaceae), *Iriartella setigera* (Mart.) H.Wendl. (Arecaceae), and *Miconia argyrophylla* DC. (Melastomataceae) (Figs. 2E, 3E).

Dense forested campinarana (DFC): forest with pronounced stratification, continuous canopy, and dense understory impairing the movement. The canopy height ranges between 10 and 16 m, with some emergent species, such as *Mauritia carana* reaching up to 20 m in height. During the wet season, the groundwater table occasionally reaches the surface, forming small ponds, which are colonized by species adapted to flooding of the root system for several months. This forest type is characterized by the dominance of palm species, such as *Euterpe catinga* Wallace (Arecaceae), *Mauritia carana*, and *Mauritiella armata* (Mart.) Burret (Arecaceae). The most frequent canopy trees are *Clusia insignis* Mart. (Clusiaceae), *Hevea rigidifolia* (Spruce ex Benth.) Müll. Arg. (Euphorbiaceae), *Iryanthera laevis* Markgr. (Myristicaceae), *Manilkara bidentata*, *Tovomita calophyllophylla* García-Villacorta & Hammel (Clusiaceae), and *Xylopia spruceana* Benth. ex Spruce (Annonaceae). The most frequent understory trees are *Adiscanthus fusciflorus* Ducke (Rutaceae), *Cybianthus amplus* (Mez) G.Agostini (Primulaceae), and *Pachira faroensis* (Ducke) W.S.Alverson (Malvaceae) (Figs. 2F, 3F).

Floristic survey. We recorded 167 species belonging to 117 genera and 50 families (Table 1; Figs. 4–8). Fabaceae (21 spp.), Rubiaceae (16 spp.), Chrysobalanaceae (11 spp.), Arecaceae, Melastomataceae, and Sapotaceae (9 spp. each), Apocynaceae and Lauraceae (6 spp. each), and Annonaceae and Clusiaceae (5 spp. each) were the most representative families in terms of the number of species (Fig. 4A). Together, these 10 families account for 58.4% of all recorded taxa. The most representative genera in terms of species numbers were *Macrolobium* Schreb. (5 spp.), followed by *Cybianthus* Mart., *Hymenopus* (Benth.) Sothers & Prance, *Ocotea* Aubl., *Palicourea* Aubl., and *Protium* Burm.f. (4 spp. each), and *Chrysophyllum* L., *Clusia* L., *Miconia* Ruiz & Pav., *Myrcia* DC., and *Remijia* DC. (3 spp. each) (Fig. 4B). Together, these 11 genera account for 24.1% of the total number of species.

Fabaceae and Rubiaceae were the richest in white-sand specialist species (8 and 7 species respectively, Fig. 4C), followed by Melastomataceae (3 spp.), Annonaceae, Araliaceae, Clusiaceae, Euphorbiaceae, Lauraceae, Malpighiaceae, and Myrtaceae (2 spp. each). Together, these 10 families account for 62.7% of the total number of white-sand specialists. When comparing the number of species in the most species-rich families in this and nine other studies carried out in campinaranas of the Brazilian Amazon, Fabaceae and Sapotaceae are cited in nine studies, Lauraceae in seven, Chrysobalanaceae and Rubiaceae in six, Annonaceae and Cluciaceae in five, and Apocynaceae in four (Table 2).

The USDR is the type locality for the recently described *Tovomita cornuta* Demarchi & L.Marinho (Clusiaceae), which has only four known populations (Demarchi et al. 2021; Fig. 6C) and is the paratype locality of *Clusia nascimentojuniorii* A.C. Alencar & Bittrich (Clusiaceae), which has only three known populations (Alencar et al. 2021; Fig 6B). Rare species are also known from USDR, including *Acmanthera minima* W.R.Anderson (Malpighiaceae), *Annona angustifolia* Huber (Annonaceae), *Croton dissectistipulatus* Secco (Euphorbiaceae), *Palicourea huberi* Steyerm. (Rubiaceae), *Remijia hirsuta* Sucre (Rubiaceae), *Sloanea*

Table 1. Checklist of the trees, treelets and shrubs from campinaranas of Uatumã Sustainable Development Reserve (Uatumã SDR), Manaus, Amazonas, Brazil. **Physiognomy:** OSC = open shrubby campinarana; DSC = dense shrubby campinarana; OAC = open arboreal campinarana; DAC = dense arboreal campinarana; OFC = open forested campinarana; DFC = dense forested campinarana. **Habitat:** gen = generalist; ohs = oligotrophic habitats specialist; wss = white-sand specialist. **Distribution:** neo = Neotropical; sam = South America; amz = Amazon basin; bam = Brazilian Amazon basin. **Vouchers:** LOD = Layon Oreste Demarchi; AR = Afonso Rabelo; JEH = John Ethan Householder; AJH = Andrew James Henderson; FMC = Flávio Magalhães Costa; CEZ = Charles Eugene Zartman; JGC-B = Jefferson Guedes de Carvalho-Sobrinho. * = Species chosen for detailed description.

Taxa	Physiognomy	Life form	Habitat	Distrib.	Vouchers
Anacardiaceae					
Tapirira guianensis Aubl.	OFC	tree	gen	neo	LOD 1456
Annonaceae					
Annona angustifolia Huber*	OSC; OAC	shrub; treelet	wss	amz	LOD 819; 1238; 1491; 1612
Guatteria aff. *duckeana* R.E. Fr.	DAC; DFC	shrub; treelet	gen	amz	LOD 1664; 1714
Guatteria schomburgkiana Mart.	OAC; OFC	tree	gen	sam	LOD 1333; 1390; 1429
Tetrameranthus duckei R.E. Fr.	OFC	treelet	wss	amz	LOD 1450; 1647
Xylopia spruceana Benth. ex Spruce*	OFC; DFC	tree	ohs	amz	LOD 1273; 1313; 1457
Apocynaceae					
Couma utilis (Mart.) Müll. Arg.	OFC	tree	gen	amz	LOD 1315
Galactophora crassifolia (Müll. Arg.) Woodson*	OSC	shrub	wss	amz	LOD 648; 811; 1164; 1221
Lacmellea arborescens (Müll. Arg.) Markgr.	OFC; DFC	tree	gen	amz	LOD 1292; 1473; 1598; 1682
Lacmellea gracilis (Müll. Arg.) Markgr.	OFC; DFC	treelet	gen	amz	LOD 1147; 1415
Macoubea sprucei (Müll. Arg.) Markgr.	OFC; DFC	tree	gen	neo	LOD 848; 1306; 1317; 1340; 1541
Tabernaemontana flavicans Willd. ex Roem. & Schult.	OAC	shrub; treelet	gen	sam	LOD 1445; 1606
Aptandraceae					
Chaunochiton angustifolium Sleumer*	OSC; DSC; OAC; DAC	tree; treelet	wss	amz	LOD 1241; 1262; 1277; 1578
Aquifoliaceae					
Ilex divaricata Mart. ex Reissek*	OSC; DSC; OAC;	shrub; treelet	wss	amz	LOD 626; 1079; 1196; 1290; 1466; 1621
Araliaceae					
Dendropanax resinosus (Marchal) Frodin	DFC	tree	wss	amz	LOD 1487
Didymopanax umbrosus (Fiaschi & Frodin) Fiaschi & G.M. Plunkett*	OFC; DFC	tree; treelet	wss	bam	LOD 354
Arecaceae					
Attalea microcarpa Mart.	OSC; OAC; OFC	palm shrub	gen	amz	AJH 635
Bactris simplicifrons Mart.	OSC; OAC	palm shrub	gen	sam	LOD 1551
Desmoncus phoenicocarpus Barb.Rodr.	DAC; DFC	palm shrub (scandent)	gen	sam	LOD 1590
Euterpe catinga Wallace*	DFC	palm treelet	ohs	amz	AR 41
Iriartella setigera (Mart.) H.Wendl.	OFC	palm treelet	gen	amz	LOD 1655
Mauritia carana Wallace*	DSC; DAC; DFC	palm tree (emergent)	ohs	amz	JEH 2321; AR 47
Mauritiella armata (Mart.) Burret	DSC; DAC; DFC	palm tree	gen	sam	AR 51
Oenocarpus minor Mart.	OFC	palm treelet	gen	amz	AR 56
Oenocarpus bataua Mart.	DFC	palm tree	gen	neo	JGC-B 1554
Asteraceae					
Lepidaploa arenaria (Mart. ex DC.) H.Rob.	OSC	shrub	ohs	sam	LOD 24; 622; 813
Gongylolepis martiana (Baker) Steyerm. & Cuatrec.*	OSC; OAC	treelet	wss	amz	LOD 170; 1274; 1321
Burseraceae					
Protium aracouchini Marchand	DFC	tree; treelet	gen	neo	LOD 1562; 1586
Protium heptaphyllum subsp. *ulei* (Swart) Daly	OSC; OAC; DAC	tree; treelet	wss	amz	LOD 1077; 1083; 1232; 1322; 1391; 1640
Protium llanorum Cuatrec.	DFC	tree	ohs	sam	LOD 1589; 1601; 1624
Protium paniculatum var. *modestum* Daly*	OFC; DFC	tree	gen	amz	LOD 1427; 1585; 1623; 1671
Calophyllaceae					
Calophyllum cf. *pachyphyllum* Planch. & Triana	DFC	tree	ohs	amz	LOD 1591
Chrysobalanaceae					
Gaulettia parillo (DC.) Sothers & Prance	OFC	tree	ohs	amz	LOD 684; 1337; 1447; 1649
Gaulettia racemosa (Benth. ex Hook. f.) Sothers & Prance	OAC; OFC	tree	gen	amz	LOD 1215; 1243; 1424; 1542; 1614
Hirtella glabrata Pilg.	DSC; DAC; OFC	tree; treelet	wss	amz	LOD 1253
Hirtella racemosa Lam. var. *racemosa*	OSC; OAC	treelet	gen	neo	LOD 106; 1076; 1552
Hymenopus laevigatus (Prance) Sothers & Prance	DFC	tree	gen	amz	LOD 1475; 1580; 1673; 1705
Hymenopus oblongifolius (Standl.) Sothers & Prance	OFC	tree (emergent)	gen	amz	LOD 1672
Hymenopus prismatocarpus (Spruce ex Hook.f.) Sothers & Prance	OFC	tree	gen	amz	LOD 1744
Hymenopus reticulatus (Prance) Sothers & Prance	OFC	tree	gen	amz	LOD 1296; 1459
Leptobalanus latus (J.F. Macbr.) Sothers & Prance*	OFC; DFC	tree	gen	amz	LOD 1074; 1403; 1482; 1618; 1683
Licania gracilipes Taub.	OFC	tree	gen	amz	LOD 281
Licania hypoleuca Benth.	OAC; DAC; OFC	tree	gen	neo	LOD 657; 1173; 1175; 1242

Taxa	Physiognomy	Life form	Habitat	Distrib.	Vouchers
Clusiaceae					
Clusia insignis Mart.	OFC; DFC	tree; hemiepiphyte	gen	sam	LOD 1307; 1308
Clusia nascimentojuniorii A.C. Alencar & Bittrich*	OSC; OAC	treelet	wss	bam	LOD 1195; 1293; 1435; 1559
Clusia nemorosa G. Mey.	OAC; DAC; DFC	tree; treelet	gen	sam	LOD 642; 1271; 1302; 1332; 1421; 1436; 1465; 1560; 1665
Tovomita calophyllophylla García-Villacorta & Hammel	DFC	tree	ohs	amz	LOD 1486; 1581; 1600; 1663
Tovomita cornuta Demarchi & L.Marinho*	DFC	treelet	wss	bam	LOD 1300; 1558; 1599; 1674
Combretaceae					
Terminalia macrophylla (Eichler) Gere & Boatwr.	OFC	tree (emergent)	gen	sam	LOD 1298; 1597
Dichapetalaceae					
Tapura lanceolata (Ducke) Rizzini*	DFC	tree	wss	amz	LOD 1395; 1464; 1498
Dilleniaceae					
Doliocarpus amazonicus subsp. *duckeanus* Kubitzki	DSC	shrub (scandent)	gen	amz	LOD 1165; 1260
Elaeocarpaceae					
Sloanea longicaudata Ducke*	DFC	tree; treelet	gen	sam	LOD 1489; 1704
Erythroxylaceae					
Erythroxylum campinense Amaral*	OFC	treelet	wss	bam	LOD 131; 1448
Euphorbiaceae					
Croton dissectistipulatus Secco*	OSC	shrub	wss	bam	LOD 25; 136; 623
Hevea rigidifolia (Spruce ex Benth.) Müll. Arg.	DFC	tree	wss	amz	LOD 1342; 1458; 1670
Mabea uleana Pax & K. Hoffm.*	OSC; OAC,	treelet	ohs	bam	LOD 123; 1146; 1256; 1545
Maprounea guianensis Aubl.	OAC	treelet	gen	neo	LOD 1407; 1423
Fabaceae					
Aldina heterophylla Spruce ex Benth.*	OSC; DSC; OAC; DAC; OFC; DFC	tree (emergent)	wss	amz	LOD 1163; 1474; 1479; 1539; 1661
Andira micrantha Ducke	DFC	tree	gen	amz	LOD 252; 253
Chamaecrista adiantifolia (Spruce ex Benth.) H.S.Irwin & Barneby var. *adiantifolia*	OFC; DFC	tree (emergent)	ohs	amz	LOD 1573
Dimorphandra campinarum Ducke*	OSC; DSC; OAC; DAC	tree; treelet	wss	bam	LOD 178; 1305; 1418; 1582; 1650
Dimorphandra pennigera Tul.	DFC	tree (emergent)	ohs	amz	LOD 1564
Diplotropis cf. *purpurea* (Rich.) Amshoff	OFC	tree	gen	neo	LOD 247
Eperua glabriflora (Ducke) R.S.Cowan*	OFC	tree	ohs	bam	CEZ 7014
Hymenolobium modestum Ducke	DFC	tree	gen	amz	LOD 245
Inga lateriflora Miq.	OFC	tree	gen	sam	LOD 1602
Macrolobium duckeanum R.S.Cowan*	DFC	tree	wss	bam	LOD 1494; 1678
Macrolobium huberianum Ducke	OSC	shrub; treelet	wss	amz	LOD 1236; 1294; 1324; 1652
Macrolobium aff. *huberianum* Ducke	OSC	shrub; treelet	na	na	LOD 1237
Macrolobium gracile Spruce ex Benth.	DAC; DFC	tree	wss	amz	LOD 1303; 1405; 1454
Macrolobium punctatum Spruce ex Benth.*	OSC; OAC	tree; treelet	wss	amz	LOD 168; 643; 660; 1363; 1370; 1493; 1561; 1651
Macrosamanea pubiramea (Steud.) Barneby & J.W.Grimes var. *pubiramea*	DFC	scandent shrub	gen	amz	LOD 1608
Ormosia discolor Spruce ex Benth.	OFC; DFC	tree	gen	amz	LOD 1574
Ormosia trifoliolata Huber	OAC; OFC; DFC	tree; treelet	wss	amz	LOD 109; 662; 1301; 1376
Parkia igneiflora Ducke*	OAC; DAC; OFC	tree (emergent)	wss	amz	LOD 1477; 1499; 1627
Parkia panurensis Benth. ex H.C.Hopkins	OFC	tree	gen	amz	LOD 1687
Swartzia brachyrachis Harms var. *brachyrachis*	DFC	tree	gen	amz	LOD 1379; 1412; 1575
Swartzia polyphylla DC.	OFC	tree	gen	amz	LOD 1439
Gentianaceae					
Potalia amara Aubl.	OFC	shrub	gen	neo	LOD 1699
Humiriaceae					
Humiria balsamifera var. *guianensis* (Benth.) Cuatrec.	OSC; OAC	Shrub; treelet	wss	amz	LOD 110; 621; 820; 1072; 1168; 1269; 1717
Sacoglottis mattogrossensis Malme	OFC; DFC	tree (emergent)	gen	sam	LOD 1318
Sacoglottis guianensis Benth.	OFC	tree	gen	sam	LOD 1596
Lamiaceae					
Vitex duckei Huber*	OSC; OAC	tree; treelet	wss	bam	LOD 627; 1325; 1372; 1557
Lauraceae					
Endlicheria arenosa Chanderb.*	OAC; OFC	tree; treelet	wss	amz	LOD 118; 1247; 1438; 1669
Mezilaurus itauba (Meisn.) Taub. ex Mez	OFC; DFC	tree (emergent)	gen	amz	LOD 1544; 1566

Taxa	Physiognomy	Life form	Habitat	Distrib.	Vouchers
Ocotea boissieriana (Meisn.) Mez	OFC	treelet	gen	amz	LOD 1422
Ocotea cf. *cernua (Nees) Mez*	OFC	tree	gen	neo	LOD 1383
Ocotea debilis Mez	OAC; OFC	tree; treelet	wss	amz	LOD 1071; 1251; 1384; 1402; 1500b; 1570;
Ocotea myriantha (Meisn.) Mez	OFC	tree	gen	amz	LOD 1382
Lecythidaceae					
Allantoma integrifolia (Ducke) S.A.Mori, Ya Y.Huang & Prance	OFC; DFC	tree (emergent)	ohs	amz	LOD 1279
Linaceae					
Hebepetalum humiriifolium (Planch.) Benth.	OAC; OFC	tree; treelet	gen	amz	LOD 1414; 1431; 1667
Malpighiaceae					
Acmanthera minima W.R.Anderson*	OSC; DSC; OAC; DAC	tree; treelet	wss	bam	LOD 1249; 1371; 1485; 1644
Byrsonima laevis Nied.	OFC; DFC	tree	wss	amz	LOD 1375; 1576; 1593
Malvaceae					
Catostemma sclerophyllum Ducke	OAC; OFC; DFC	tree	ohs	amz	LOD 1385
Pachira faroensis (Ducke) W.S.Alverson*	DFC	tree	wss	amz	LOD 1588; 1625
Scleronema micranthum (Ducke) Ducke	OFC	tree	gen	amz	LOD 1240
Melastomataceae					
Henriettea granulata Berg ex Triana	OAC; DAC; DFC	shrub; treelet	ohs	amz	LOD 1584; 1718
Macairea theresiae Cogn.*	OSC; DSC; OAC; DAC	shrub; treelet	wss	bam	LOD 1233
Miconia argyrophylla DC.	OAC; OFC	treelet	gen	neo	LOD 1336; 1416; 1595; 1611
Miconia gratissima Benth. ex Triana	DAC	shrub; treelet	gen	neo	LOD 1657
Miconia subsimplex Pilg.*	OAC; OFC	shrub; treelet	wss	bam	LOD 1184; 1555
Mouriri nervosa Pilger	OFC; DFC	shrub; treelet	gen	amz	LOD 644; 1543; 1569
Sandemania hoehnei (Cogn.) Wurdack	OSC	shrub	wss	amz	LOD 1217
Tococa macrosperma Mart.	DAC; DFC	shrub	gen	sam	LOD 1449
Tococa nitens (Benth.) Triana	DAC; DFC	shrub	ohs	sam	FMC 1856
Meliaceae					
Trichilia cipo (A.Juss.) C.DC.	OFC	tree	gen	neo	LOD 1299
Metteniusaceae					
Emmotum orbiculatum (Benth.) Miers	OSC; DSC; OAC; DAC	tree; treelet	ohs	sam	LOD 139; 619; 815; 1078; 1169; 1326; 1437; 1565
Moraceae					
Ficus mathewsii (Miq.) Miq.	OSC; DSC	tree; hemiepiphyte	gen	sam	LOD 1366
Ficus trigona L.f.	OSC; DSC	tree; hemiepiphyte	gen	sam	LOD 1216
Myristicaceae					
Iryanthera laevis Markgr.	DFC	tree	gen	amz	LOD 1343; 1583; 1668
Myrtaceae					
Eugenia biflora (L.) DC.	OSC; OAC	shrub; treelet	gen	neo	LOD 1571
Myrcia citrifolia (Aubl.) Urb.	OSC; OAC	shrub; treelet	gen	neo	LOD 1252; 1266; 1330; 1410; 1642
Myrcia saxatilis (Amshoff) McVaugh	OAC; DAC; OFC; DFC	treelet	wss	amz	LOD 1367; 1377; 1420
Myrcia servata McVaugh	OFC	treelet	wss	amz	LOD 1688
Nyctaginaceae					
Neea obovata Spruce ex Heimerl	OSC; OAC; OFC	tree; treelet	gen	sam	LOD 1082; 1368; 1392; 1609; 1643; 1702
Ochnaceae					
Ouratea spruceana Engl.*	OSC; OAC; OFC	tree; treelet	wss	amz	LOD 119; 137; 620; 1255; 1378
Olacaceae					
Dulacia candida (Poepp.) Kuntze	OFC	treelet	gen	sam	LOD 1172; 1219; 1495; 1666
Ptychopetalum olacoides Benth.	OFC	tree	gen	amz	LOD 1470; 1490
Opiliaceae					
Agonandra silvatica Ducke	DFC	tree	gen	amz	LOD 1396
Pentaphylacaceae					
Ternstroemia dentata (Aubl.) Sw.	OAC; OFC	tree	gen	amz	LOD 1069; 1248; 1406
Ternstroemia pungens Gleason*	OSC; DSC; OAC; DAC	shrub	wss	amz	LOD 172; 624; 1148; 1646
Peraceae					
Pera bicolor (Klotzsch) Müll.Arg.	OFC; DFC	tree	gen	amz	LOD 1309; 1709
Pogonophora schomburgkiana Miers ex Benth.	OAC	tree	gen	sam	LOD 1413
Polygalaceae					
Bredemeyera myrtifolia (A.W.Benn.) Marques	OSC; OAC	scandent shrub	gen	amz	LOD 1166; 1289; 1365
Securidaca retusa Benth.	DSC; DAC	scandent shrub	ohs	amz	LOD 180; 1272; 1310; 1700
Polygonaceae					
Coccoloba parimensis Benth.	OSC; OAC	scandent shrub	gen	neo	LOD 1250; 1259; 1276; 1362; 1389; 1654
Primulaceae					
Cybianthus amplus (Mez) G.Agostini	DFC	treelet	ohs	sam	LOD 1455; 1463; 1480; 1496

Taxa	Physiognomy	Life form	Habitat	Distrib.	Vouchers
Cybianthus fulvopulverulentus (Mez) G.Agostini	OSC; DSC; OAC; DAC; OFC; DFC	tree; treelet	gen	sam	LOD 1267; 1329
Cybianthus fulvopulverulentus subsp. *magnoliifolius* (Mez) Pipoly	OFC; DFC	tree; treelet	gen	amz	LOD 1335
Cybianthus reticulatus (Benth. ex Miq.) G.Agostini	OSC; OAC	treelet	ohs	amz	LOD 1257; 1328; 1546; 1554; 1605
Rhabdodendraceae					
Rhabdodendron macrophyllum (Spruce ex Benth.) Huber*	OFC; DFC	treelet	wss	bam	LOD 832; 1497
Rhizophoraceae					
Sterigmapetalum plumbeum Aymard & Cuello*	OAC; OFC	tree (emergent)	wss	bam	LOD 1312; 1409
Rubiaceae					
Duroia saccifera (Schult. & Schult.f.) K.Schum.	OFC	treelet	gen	amz	LOD 1388; 1441
Ferdinandusa guainiae Spruce ex K.Schum.	OFC	tree	ohs	sam	LOD 1144; 1246; 1331; 1432; 1537
Ixora intensa K.Krause	OSC; OAC	shrub; treelet	wss	amz	LOD 1258; 1472; 1536; 1613
Kutchubaea oocarpa (Spruce ex Standl.) C.H.Perss.	OAC; OFC	treelet	gen	amz	LOD 834; 1440; 1610
Kutchubaea sericantha Standl.	OFC	tree	gen	amz	LOD 377; 378
Pagamea coriacea Spruce ex Benth.	OSC; DSC; OAC; DAC	tree; treelet	wss	amz	LOD 1081; 1171; 1430; 1553; 1577; 1711
Pagamea guianensis Aubl.	OAC	tree; treelet	ohs	sam	LOD 177
Palicourea blakei (Standl. &Steyerm) Borhidi*	OSC; OAC	shrub	wss	amz	LOD 1399; 1659
Palicourea hoffmannseggiana (Willd. ex Schult.) Borhidi	OAC; OFC	shrub	gen	neo	LOD 1408; 1630
Palicourea huberi Steyerm.*	OAC; OFC	shrub	ohs	amz	LOD 1234; 1710
Palicourea nitidella (Müll.Arg.) Standl.	OSC; OAC	shrub	ohs	amz	LOD 1073; 1075; 1400; 1708
Remijia amazonica K.Schum.	OAC	treelet	gen	amz	LOD 1304; 1567; 1680
Remijia hirsuta Sucre*	OFC; DFC	treelet	wss	bam	LOD 1316; 1426; 1660; 1679
Remijia morilloi Steyerm.*	DSC	shrub; treelet	wss	amz	LOD 181; 1170; 1467; 1645
Retiniphyllum schomburgkii (Benth.) Müll.Arg.	OSC; OAC	shrub	wss	amz	LOD 1244; 1327; 1434; 1639
Semaphyllanthe obovata (Ducke) L.Andersson	DSC; DAC	treelet	wss	amz	LOD 1401; 1715
Rutaceae					
Adiscanthus fusciflorus Ducke	DAC; DFC	treelet	wss	amz	LOD 1361; 1454; 1626
Hortia longifolia Spruce ex Engl.*	OFC	tree; treelet	gen	bam	LOD 1540
Sapindaceae					
Matayba inelegans Spruce ex Radlk.	OAC; OFC	tree; treelet	gen	sam	LOD 381; 1254; 1381; 1563
Matayba opaca Radlk.	OSC; OAC; OFC	tree; treelet	ohs	sam	LOD 842; 1151; 1468; 1675
Talisia ghilleana Acev.-Rodr.*	OSC; OAC	shrub; treelet	wss	bam	LOD 685; 1278; 1394; 1425; 1579; 1701
Sapotaceae					
Chrysophyllum cf. *amazonicum* T.D.Penn.	OFC	tree	gen	amz	LOD 1488
Chrysophyllum pomiferum (Eyma) T.D.Penn.	DFC	tree (emergent)	gen	amz	LOD 1399
Chrysophyllum sanguinolentum subsp. *balata* (Ducke) T.D.Penn.	OFC	tree (emergent)	gen	amz	LOD 1538; 1689
Elaeoluma aff. *glabrescens* (Mart. & Eichler) Aubrév.	DFC	tree	ohs	amz	LOD 1220; 1320; 1476
Elaeoluma schomburgkiana (Miq.) Baill.	OSC; OAC; OFC	tree; treelet	ohs	amz	LOD 1314; 1404; 1483; 1492
Manilkara bidentata (A.DC.) A.Chev.	OFC; DFC	tree (emergent)	gen	neo	LOD 828; 1235; 1297; 1338; 1658
Pouteria cuspidata (A.DC.) Baehni	OFC	tree	gen	neo	LOD 1592
Pouteria scrobiculata Monach. ex T.D.Penn.	OFC	tree	ohs	amz	LOD 1334
Pradosia schomburgkiana (A.DC.) Cronquist*	OSC; OAC; OFC	tree; treelet	wss	amz	LOD 1397; 1484; 1620; 1681; 1716
Simaroubaceae					
Simaba guianensis Aubl.	OSC; OAC; OFC	tree	gen	sam	LOD 810; 1145; 1183; 1587
Simaba aff. *guianensis* Aubl.	OFC	treelet	na	na	LOD 1380; 1411
Simarouba amara Aubl.	OAC; OFC	tree; treelet	gen	neo	LOD 1323
Vochysiaceae					
Ruizterania retusa (Spruce ex Warm.) Marc.-Berti	OAC; OFC	tree (emergent)	ohs	amz	LOD 1280
Vochysia obscura Warm.	OFC	tree	gen	amz	LOD 1393

longicaudata Ducke (Elaeocarpaceae), and *Sterigmapetalum plumbeum* (Rhizophoraceae), which all have fewer than 10 specimens in herbaria worldwide.

Concerning the distribution of species, 20 species (12%) have a Neotropical distribution (neo), 29 species (17.4%) are distributed in South America (sam), the majority of species (98 spp, 58.7%) occur in the Amazon basin (amz), and 18 species (10.8%) are restricted to the Brazilian Amazon (bam) (Fig. 4D). Concerning habitat preferences, 86 species (51.5%) are generalists (gen), occurring in various types of habitats; 29 species (17.4%) are oligotrophic habitat specialists (ohs) occurring in campinarana and igapós habitats, and 50 species (29.9%) were considered white-sand specialists (wss) occurring only in Amazonian campinaranas.

Through observations made over seven years of systematic field expeditions and consultation of the previously specified database, we provide descriptions, distribution, phenological, and habitat information of all species that were classified as endemic to the Brazilian Amazon (bam), white-sand specialists considered rare (with less than 10 specimens recorded in herbaria),

Table 2. Comparison between studies developed in campinarana areas in the Brazilian Amazon. **Sampling criteria:** DBH = Diameter at breast height; DGH = Diameter at ground height. **Most representative families:** Ann = Annonaceae; Apo = Apocynaceae; Are = Arecaceae; Bur = Burseraceae; Chr = Chrysobalanaceae; Clu = Clusiaceae; Eup = Euphorbiaceae; Fab = Fabaceae; Lau = Lauraceae; Lec = Lecythidaceae; Mal = Malpighiaceae; Malv = Malvaceae; Mel = Melastomataceae; Mor = Moraceae; Myri = Myristicaceae; Myr = Myrtaceae; Och = Ochnaceae; Pen = Pentaphylacaceae; Rub = Rubiaceae; Sapi = Sapindaceae; Sap = Sapotaceae. (*) indicates that floristic sampling was also conducted outside the plots for the preparation of species lists.

Reference	No. of families	No. of genera	No. of species	Sampled area (ha)	Sampling criteria (cm)	Most representative families
Boubli 2002	27	52	60	0.5	DBH ≥ 10	Fab., Rub., Sap., Clu., Eup., Lau., Lec.,
Campos 2017	57	170	324	6.2	DBH ≥ 2.5	Fab., Sap., Rub., Lau., Ann., Chr., Bur., Are., Apo., Clu.
Demarchi et al. 2018	40	86	140	2.25	DBH ≥ 5	Fab., Sap., Lau., Bur., Mor., Myr., Sapi., Apo., Rub., Clu., Chr.
Farroñay 2019	46	118	205	0.3	DBH ≥ 1	Fab., Lau., Chr., Rub., Bur., Myr., Ann., Are., Sap., Mel.
Ferreira 1997	30	67	117	1.0	DBH ≥ 5	Fab., Sap., Lau., Mel., Rub., Bur., Chr., Sapi., Apo.
Gomes and Pinto 2015	9	12	12	0.3	DBH ≥ 5	Fab., Sap., Pen., Och., Lau., Ann., Bur.
Stropp et al. 2011	39	124	290	3.0	DBH ≥ 10	Fab., Sap., Eup., Ann., Bur., Clu., Chr., Myri., Mor., Lec.
Targhetta et al. 2015	38	87	122	3.0	DBH ≥ 10	Fab., Sap., Chr., Apo., Are., Malv., Myri.
Vicentini 2004*	38	78	110	0.47	DBH ≥ 2.5	Fab., Rub., Sap., Lau., Clu., Bur., Mal., Mel., Ann., Eup.
This study*	50	117	167	3.0	DGH ≥ 5 / DBH ≥ 10	Fab., Rub., Chr., Sap., Are., Mel., Apo., Lau., Ann., Clu.

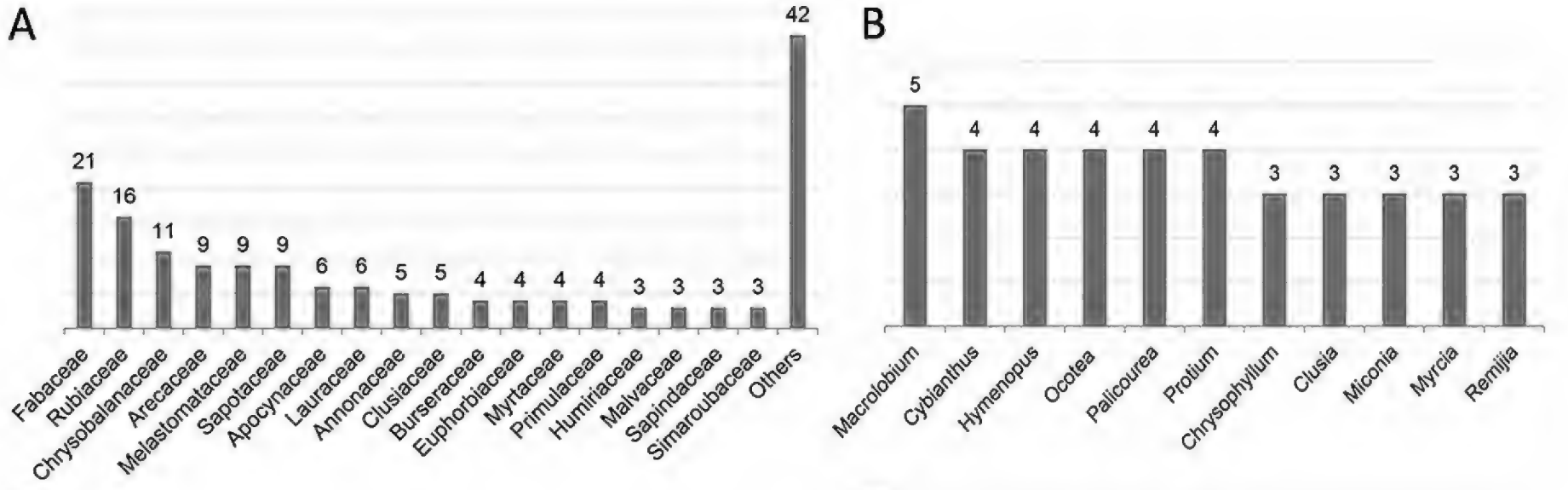

Figure 4. Numbers of species from campinaranas of Uatumã Sustainable Development Reserve by families, genera, habitat occurrence and distribution. **A.** Number of species of the richest families. **B.** Number of species of the richest genera. **C.** Families sorted according to the richness of white-sand specialist species (wss), the number of oligotrophic habitat specialist (ohs), and generalist species (gen). **D.** Number of species by distribution category.

abundant, and representative according to the inventories of the PELD MAUA project.

***Annona angustifolia* Huber**

Figure 5A

Botanical family. Annonaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′56.02″S, 059°01′19.81″W; alt. 40 m; 20.IV.2017; L.O. Demarchi 819 leg.; INPA 277930. • ibid.; 08.VII.2018; L.O. Demarchi 1238 leg.; INPA 288393. • ibid.; 14.IV.2019; L.O. Demarchi 1491 leg.; INPA 288615. • ibid.; 10.XI.2019; L.O. Demarchi 1612 leg.; INPA 288692.

Geographic distribution. Amazon basin. Occurs in Brazil and Bolivia. In Brazil, this species occurs in the states of Amazonas and Pará.

Identification. Shrub or treelet, 2–4 m high. Leaves alternate distichous, membranaceous, lanceolate, apex cuspidate, base sometimes asymmetric, acute to obtuse; venation brochidodromous. Solitary flowers, sepals 3, suborbiculate; petals 3 white, ovate.

Habitat and phenological observations. This species occurs in small islands of vegetation formed by sparse trees (OSC), and in the understory of arboreal

physiognomies (OAC) with elevated light penetration. Observed in flowers predominantly from February to April and fruits between May and October.

***Xylopia spruceana* Benth. ex Spruce**
Figure 5B

Botanical family. Annonaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′25.98″S, 059° 01′17.32″W; alt. 40 m; 16.VII.2018; L.O. Demarchi 1273 leg.; INPA 288428. • ibid.; 06.IX.2018; L.O. Demarchi 1313 leg.; INPA 288463. • ibid.; 16.XII.2018; L.O. Demarchi 1457 leg.; INPA 288583.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, and Venezuela. In Brazil, this species occurs only in the state of Amazonas.

Identification. Tree, 10–20 m high. Leaves alternate distichous, elliptic to oblongate, apex emarginate to retuse, base asymmetric, cuneate or truncate, abaxial surface glabrous to sparsely sericeous on the central veins; secondary veins inconspicuous. Inflorescences axillary or ramiflorous; flowers 2–3, sepals 3, connate at the base, petals 3, strictly oblong to softly cochleariform.

Habitat and phenological observations. This species occurs predominantly in forested areas with seasonal inundation by an elevated groundwater tables (DFC), often occupying the canopy of this physiognomy. Observed with flowers from August to September and fruits between October and January.

***Galactophora crassifolia* (Müll.Arg.) Woodson**
Figure 5C

Botanical family. Apocynaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′56.02″S, 059° 01′19.81″W; alt. 40 m; 01.IX.2015; L.O. Demarchi 648 leg.; INPA 274275. • ibid.; 20.IV.2017; L.O. Demarchi 811 leg.; INPA 277922. • ibid.; 29.IV.2018; L.O. Demarchi 1164 leg.; INPA 288359. • ibid.; 02.VI.2018; L.O. Demarchi 1221 leg.; INPA 288385.

Geographic distribution. Amazon basin. Occurs in Brazil, Bolivia, Colombia, Peru, and Venezuela. In Brazil, this species occurs in the states of Amazonas, Pará, Rondônia, and Mato Grosso.

Identification. Shrub, 1–2 m high. Leaves opposite decussate, subcoriaceous to coriaceous, sessile to subsessile, ovate to elliptic, apex obtuse to mucronate, base subcordate, margin revolute, sparsely papillous or glabrescent on both surfaces; venation brochidodromous. Inflorescences terminal to subterminal; flowers 1–5; sepals with lacinias ovate-lanceolate to ovate-elliptic; petals white to pinkish, campanulate at the apex.

Habitat and phenological observations. This species occurs exclusively in open physiognomies exposed to full solar radiation (OSC). Observed with flowers from April to June and fruits between July and September.

***Chaunochiton angustifolium* Sleumer**
Figure 5D

Botanical family. Aptandraceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′56.02″S, 059°01′ 19.81″W; alt. 40 m; 08.VII.2018; L.O. Demarchi 1241 leg.; INPA 288396. • ibid.; 14.VII.2018; L.O. Demarchi 1262 leg.; INPA 288417. • ibid.; 02.IX.2018; L.O. Demarchi 1277 leg.; INPA 288432. • ibid.; 14.IX.2019; L.O. Demarchi 1578 leg.; INPA 288664.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, and Venezuela. In Brazil, this species occurs in the states of Amazonas and Roraima.

Identification. Treelet or tree, 2–12 m high. Leaves alternate distichous, coriaceous, lanceolate to obovate, apex obtuse to rounded, base acute; venation brochidodromous. Inflorescences axillary, with 10–15 flowers per panicle, calyx cupuliform, petals 5, greenish to yellow.

Habitat and phenological observations. This species occupies shrubby physiognomies exposed to full solar radiation (OSC and DSC) or in the canopy of arboreal physiognomies (OAC and DAC) with an elevated or deep groundwater table. Observed with flowers from June to September and fruits between September and October.

***Ilex divaricata* Mart. ex Reissek**
Figure 5E

Botanical family. Aquifoliaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′56.02″S, 059° 01′19.81″W; alt. 40 m; 28.VIII.2015; L.O. Demarchi 626 leg.; INPA 274253. • ibid.; 08.XI.2017; L.O. Demarchi 1079 leg.; INPA 288338. • ibid.; 05.V.2018; L.O. Demarchi 1196 leg.; INPA 288378. • ibid.; 02.IX.2018; L.O. Demarchi 1290 leg.; INPA 288441. • ibid.; 11.I.2019; L.O. Demarchi 1466 leg.; INPA 288592. • ibid.; 12.XII.2019; L.O. Demarchi 1621 leg.; INPA 288701.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, and Venezuela. In Brazil, this species occurs in the states of Acre, Amazonas, Pará, Rondônia, Roraima, and Mato Grosso.

Identification. Shrub or treelet, 2–5 m high. Leaves alternate spiral, coriaceous, elliptic to spatulate, apex emarginate to obtuse, base rounded to acute, margin revolute; venation brochidodromous. Inflorescences fasciculate, pistillate and staminate in clusters of dicasium, formed by 3 flowers; sepals 4, glabrous, petals 4, white.

Habitat and phenological observations. This species preferentially occurs in open physiognomies (OSC and OAC); it also occurs in areas with an elevated groundwater table and exposed to full solar radiation (DSC). Observed with flowers from September to December and fruits between November and March.

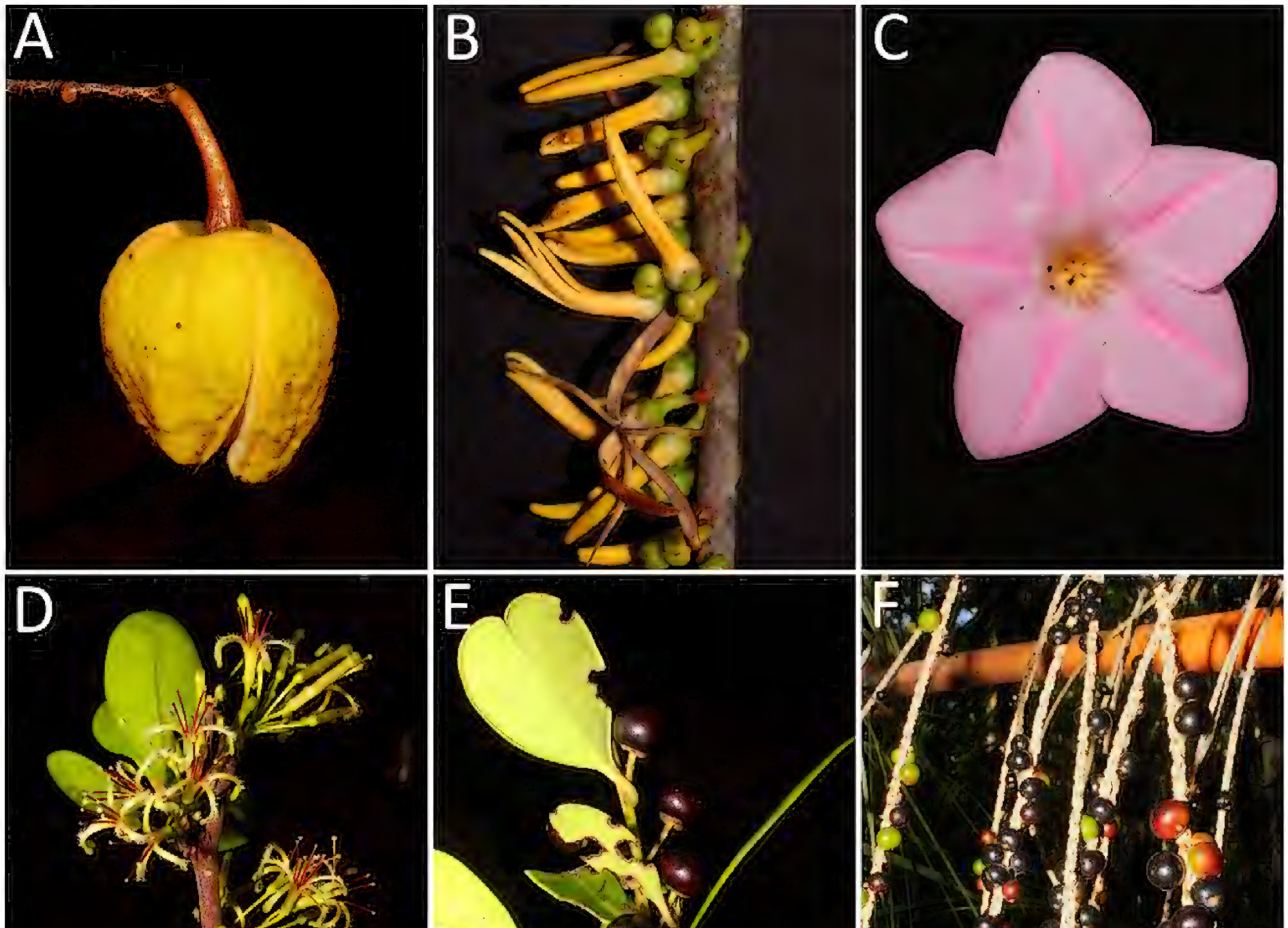

Figure 5. Some species from campinaranas of Uatumã Sustainable Development Reserve. **A.** *Annona angustifolia* (Annonaceae), flower. **B.** *Xylopia spruceana* (Annonaceae), buds and flowers. **C.** *Galactophora crassifolia* (Apocynaceae), flower. **D.** *Chaunochiton angustifolium* (Aptandraceae), flowers. **E.** *Ilex divaricata* (Aquifoliaceae), mature fruits. **F.** *Euterpe catinga* (Arecaceae), immature and mature fruits. **G.** *Mauritia carana* (Arecaceae), mature fruits. **H.** *Gongylolepis martiana* (Asteraceae), flowers. **I.** *Protium paniculatum* var. *modestum* (Burseraceae), mature fruits.

***Didymopanax umbrosus* (Fiaschi & Frodin) Fiaschi & G.M.Plunkett**

Botanical family. Araliaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′15.03″S, 059°01′20.71″W; alt. 40 m; 09.VI.2013; L.O. Demarchi 354 leg.; EAFM 11203, INPA 262115.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs in the states of Amazonas and Pará.

Identification. Treelet or tree, 4–8 m high. Leaves alternate spiral, compound, digitate, top-concentrated; leaflets 8–10, elliptic to ovate, base rounded to obtuse, apex caudate, abaxial surface sericeous and ochraceous; venation brochidodromous. Inflorescences terminal, umbeliform, with 15–25 flowers; petals 5, greenish.

Habitat and phenological observations. This species occurs in the understory of forested physiognomies (OFC and DFC) in areas with deep or elevated groundwater table. Observed with flowers from April to May and fruits in June.

***Euterpe catinga* Wallace**

Figure 5F

Botanical family. Arecaceae

Material examined. BRAZIL – **Amazonas** • Presidente Figueiredo, Vila Balbina; 02°03′10″S, 059°23′40″W; 25.XI.1996; A. Rabelo 41 leg.; INPA 190392.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, Ecuador, Guiana, Peru, and Venezuela. In Brazil, this species occurs in the states of Acre and Amazonas.

Identification. Palm treelet, 3–8 m high. Stalk solitary to occasionally cespitous. Leaves pinnate; sheaths closed, orange, reddish or greenish, usually with a mass of black fibers at the apex; foliar segments regularly distributed and at the same plane. Inflorescences infrafoliolar; staminate and pistillate flowers with sepals and petals ovate.

Habitat and phenological observations. This species occurs exclusively in the understory of forest physiognomies with an elevated groundwater table (DFC). Observed with flowers from April to June and fruits between July and December.

***Mauritia carana* Wallace**

Figure 5G

Botanical family. Arecaceae

Material examined. BRAZIL – **Amazonas** • Presidente Figueiredo, RDS Uatumã; 01°58′56″S, 059°27′25″W; 27.XI.2012; J.E. Householder 2321 leg.; INPA 269003. • Amazonas: Presidente Figueiredo, Vila Balbina; 02°03′10″S, 059°23′40″W; 26.XI.1996; A. Rabelo 47 leg.; INPA 190398.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, Peru, and Venezuela. In Brazil, this species occurs in the states of Amazonas and Roraima.

Identification. Palm tree, 8–28 m high. Stalk solitary. Leaves flabeliform; sheaths open, with many long fibers at the margins; petiole with fibers at the base; foliar segments pendulous at the apex, with spines at the margins. Inflorescences interfoliolar. Pistillate flowers bigger than staminate ones. This species is highly similar to *Mauritia flexuosa* in terms of plant shape, but is easily distinguished by the pendulous foliar segments and the fibers at the sheaths and at the base of petioles.

Habitat and phenological observations. This species occurs in the canopy or as an emergent tree, in shrubby, arboreal, and forested physiognomies (DSC, DAC, and DFC) with an elevated groundwater table. Observed with flowers from August to October and fruits between September and March.

***Gongylolepis martiana* (Baker) Steyerm. & Cuatrec.**

Figure 5H

Botanical family. Asteraceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′56.02″S, 059°01′19.81″W; alt. 40 m; 02.VIII.2014; L.O. Demarchi 170 leg.; INPA 268638. • ibid.; 16.VII.2018; L.O. Demarchi 1274 leg.; INPA 288429. • ibid.; 06.IX.2018; L.O. Demarchi 1321 leg.; INPA 288470.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, and Venezuela. In Brazil, this species occurs in the states of Amazonas and Roraima.

Identification. Treelet, 2–5 m high. Leaves alternate spiral, coriaceous, oblong to oblanceolate, apex emarginate to rounded, base attenuate; venation reticulate. Inflorescences corymbiform. Flowers 9–18, campanulate, reddish to vinaceous.

Habitat and phenological observations. This species occurs in the open shrubby and arboreal physiognomies (OSC and OAC), exposed to full solar radiation or in the understory with elevated light intensity. Observed with flowers between January to February and from August to September and fruits in March and between September and October.

***Protium paniculatum* var. *modestum* Daly**

Figure 5I

Botanical family. Burseraceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′29.86″S, 059°01′12.97″W; alt. 40 m; 09.XII.2018; L.O. Demarchi 1427 leg.; INPA 288554. • ibid.; 14.IX.2019; L.O. Demarchi 1585 leg.; INPA 288669. • ibid.; 12.XII.2018; L.O. Demarchi 1623 leg.; INPA 288703. • ibid.; 10.II.2020; L.O. Demarchi 1671 leg.; INPA 288740.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, and Venezuela. In Brazil, this species occurs in the states of Amazonas and Rondônia.

Identification. Tree, 8–16 m high. Leaves alternate spiral, compound, imparipinnate, 1–2(–3) jugate; basal

leaflets elliptic and slightly falcate, terminal leaflet elliptic to obovate; apex acuminate, base asymmetric; venation brochidodromous. Inflorescences with flowers in both sexes, petals greenish. This species is similar to others *Protium* species of the area, but is easily distinguished by leaflets with whitish abaxial face and erect inflorescence with 6–20 cm long.

Habitat and phenological observations. This species occurs in the sub-canopy of forested physiognomies (OFC and DFC) in areas with deep or elevated groundwater table. Observed with flowers from September to November and fruits between November and March.

***Leptobalanus latus* (J.F.Macbr.) Sothers & Prance**
Figure 6A

Botanical family. Chrysobalanaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′04.16″S, 059° 01′06.52″W; alt. 40 m; 08.XI.2017; L.O. Demarchi 1074 leg.; INPA 288333. • ibid.; 04.XI.2018; L.O. Demarchi 1403 leg.; INPA 288532. • ibid.; 08.III.2019; L.O. Demarchi 1482 leg.; INPA 288607. • ibid.; 12.XII.2019; L.O. Demarchi 1618 leg.; INPA 288698. • ibid.; 11.III.2020; L.O. Demarchi 1683 leg.; INPA 288751.

Geographic distribution. Amazon basin. Occurs in Brazil, Bolivia, Colombia, Ecuador, French Guiana, Peru, and Venezuela. In Brazil, this species occurs in the state of Amazonas with possible occurrences in the states of Acre and Rondônia.

Identification. Tree, 6–15 m high. Leaves alternate distichous, coriaceous, oblong-elliptic, apex acuminate, base rounded to cuneate, glabrous on adaxial surface and with pulverulent pubescence on abaxial surface; 2 glands at the lamina base on abaxial surface; venation brochidodromous. Inflorescences paniculate terminal and axillary, with 20–35 flowers per raceme; flowers sessile on primary branches or grouped on short peduncles; bracts and bracteoles ovate, persistent; sepals with acute lobes; petals absent. In the area, this species is similar to *Licania* and *Hymenopus* species, but is easily distinguished by the spherical fruits.

Habitat and phenological observations. Typical subcanopy species, occupying forest physiognomies with deep or elevated groundwater table (OFC and DFC). Observed with flowers from November to January and fruits between January and March.

***Clusia nascimentojuniorii* A.C. Alencar & Bittrich**
Figure 6B

Botanical family. Clusiaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′56.02″S, 059° 01′19.81″W; alt. 40 m; 04.V.2018; L.O. Demarchi 1195 leg.; INPA 288377. • ibid.; 02.IX.2018; L.O. Demarchi 1293 leg.; INPA 288444. • ibid.; 09.XII.2018; L.O. Demarchi 1435 leg.; INPA 288562. • ibid.; 11.VIII.2019; L.O. Demarchi 1559 leg.; INPA 288646.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs only in the state of Amazonas.

Identification. Treelet, 2–6 m high. Leaves opposite decussate, coriaceous to subcoriaceous, obovate to elliptic, apex obtuse to rounded, base acute to acuminate, margin revolute; secondary venation inconspicuous. Inflorescences cymose, erect, with 3–9 flowers; sepals 4–5, petals 4–8, white. This species is similar to others *Clusia* species of the area, but is easily distinguished by smaller leaves and 5-lobed fruits (7 or more lobes in *C. nemorosa* and 6 lobes in *C. insignis*).

Habitat and phenological observations. This species occurs in the small islands of vegetation of the shrubby physiognomies (OSC), and it also occurs as treelets in the arboreal physiognomies (OAC), not tolerating shade. Observed with flowers from August to October and fruits between September and March.

***Tovomita cornuta* Demarchi & L.Marinho**
Figure 6C

Botanical family. Clusiaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′29.86″S, 059° 01′12.97″W; alt. 40 m; 04.IX.2018; L.O. Demarchi 1300 leg.; INPA 287888. • ibid.; 11.VIII.2019; L.O. Demarchi 1558 leg.; INPA 287889. • ibid.; 10.X.2019; L.O. Demarchi 1599 leg.; INPA 287890. • ibid.; 10.III.2020; L.O. Demarchi 1674 leg.; INPA 287891.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs only in the state of Amazonas.

Identification. Treelet, 4–8 m high. Leaves opposite decussate, subcoriaceous, oblong to obovate, apex acuminate to cuneate, base obtuse to rounded, margin slightly revolute; venation brochidodromous. Inflorescences cymose, staminate with 20–50 flowers, and pistillate with 7–8 flowers; sepals 2, greenish to white, petals 4, greenish to white. In the area, this species is similar to *Tovomita calophyllophylla*, but is easily distinguished by the free and dilated styles on the fruit.

Habitat and phenological observations. This species occurs exclusively in the understory of forest physiognomies with an elevated groundwater table (DFC). Observed with flowers from August to October and fruits between October and March.

***Tapura lanceolata* (Ducke) Rizzini**

Botanical family. Dichapetalaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′ 52.72″S, 059° 01′10.84″W; alt. 40 m; 03.XI.2018; L.O. Demarchi 1395 leg.; INPA 288524. • ibid.; 11.I.2019; L.O. Demarchi 1464 leg.; INPA 288590. • ibid.; 14.IV.2019; L.O. Demarchi 1498 leg.; INPA 288622.

Geographic distribution. Amazon basin. Occurs in Brazil and Colombia. In Brazil, this species occurs only in the state of Amazonas.

Identification. Tree, 10–20 m high. Leaves alternate,

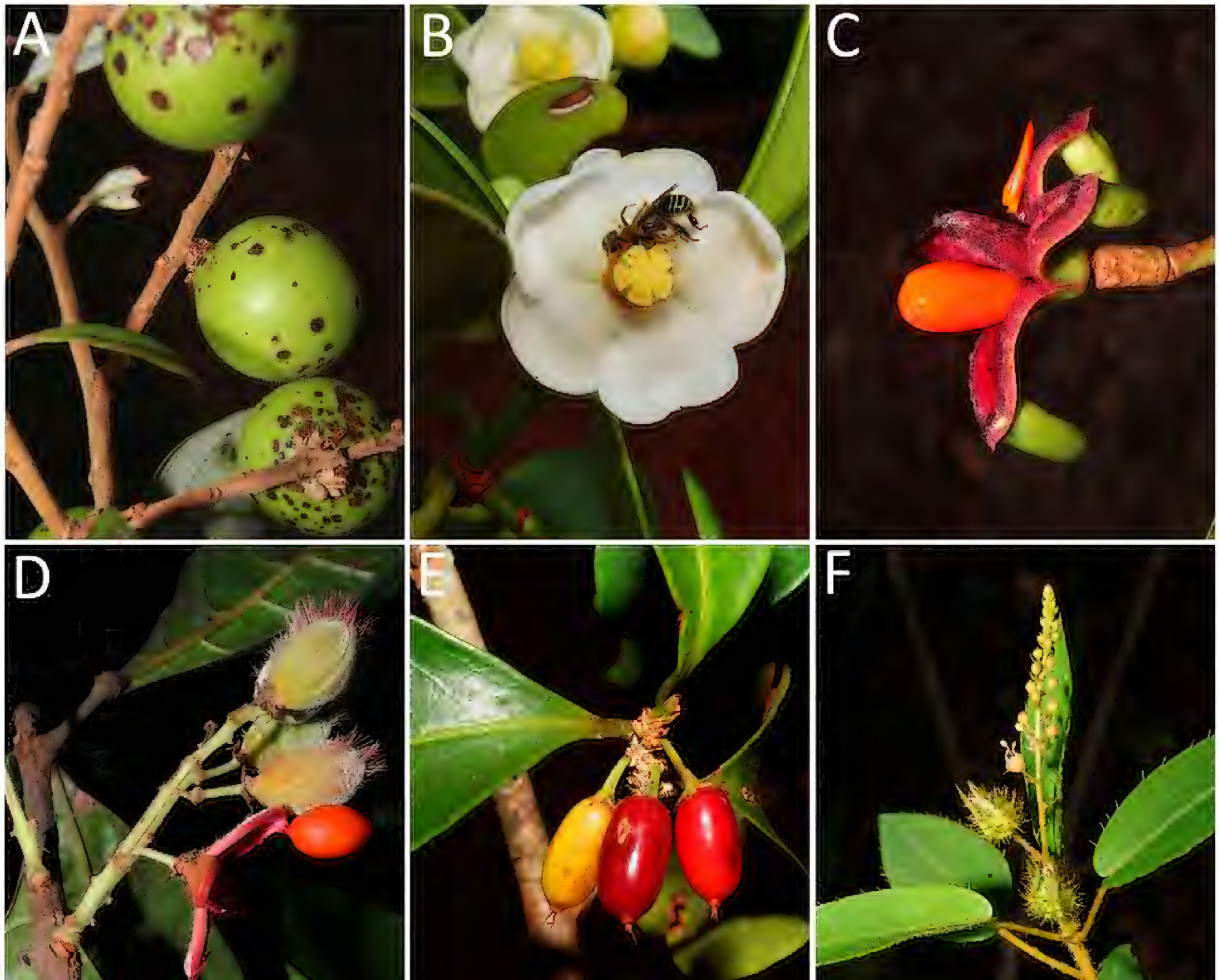

Figure 6. Some species from campinaranas of Uatumã Sustainable Development Reserve. **A.** *Leptobalanus latus* (Chrysobalanaceae), mature fruits. **B.** *Clusia nascimentojuniorii* (Clusiaceae), flowers. **C.** *Tovomita cornuta* (Clusiaceae), mature fruits. **D.** *Sloanea duckei* (Elaeocarpaceae), mature fruits. **E.** *Erythroxylum campinense* (Erythroxylaceae), mature fruits. **F.** *Croton dissectistipulatus* (Euphorbiaceae), flowers and immature fruits. **G.** *Mabea uleana* (Euphorbiaceae), mature fruits. **H.** *Aldina heterophylla* (Fabaceae), buds and flowers. **I.** *Dimorphandra campinarum* (Fabaceae), flowers.

elliptic to oblong, apex acuminate, base rounded to cuneate; venation brochidodromous. Inflorescences sessile, attached to petiole, with 8–15 flowers, at the apex of the petiole; petals connate, 5-lobate.

Habitat and phenological observations. This species generally occupies the sub-canopy of forested physiognomies with an elevated groundwater table (DFC). Observed with flowers from November to January and fruits between February and April.

***Sloanea longicaudata* Ducke**
Figure 6D

Botanical family. Elaeocarpaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′29.86″S, 059° 01′12.97″W; alt. 40 m; 14.IV.2019; L.O. Demarchi 1489 leg.; INPA 288613. • ibid.; 24.XI.2020; L.O. Demarchi 1704 leg.; INPA 289082.

Geographic distribution. South America. In Brazil, this species occurs in the states of Amazonas, Pará, Mato Grosso, and Bahia.

Identification. Treelet or tree, 6–10 m high. Leaves alternates to sub-opposite, elliptic, apex obtuse to acuminate, base cuneate; venation eucamptodromous. Inflorescence axillary or ramifloral, with 5–12 flowers, persistent bracteoles. Flowers with 4–6 sepals, white.

Habitat and phenological observations. This species generally occupy the understory or the sub-canopy of forested physiognomies with an elevated groundwater table (DFC). Observed with flowers from December to January and fruits between January and April.

***Erythroxylum campinense* Amaral**
Figure 6E

Botanical family. Erythroxylaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′15.03″S, 059° 01′20.71″W; alt. 40 m; 02.VIII.2014; L.O. Demarchi 131 leg.; INPA 268604. • ibid.; 12.XII.2018; L.O. Demarchi 1448 leg.; INPA 288575.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs only in the state of Amazonas.

Identification. Treelet, 2–4 m high. Leaves alternate distichous, coriaceous, obovate, apex retuse to short-acuminate, base cuneate to acuminate; venation brochidodromous. Flowers solitary axillary, congested. Sepals with triangular lobes, petals oblong-elliptic, white.

Habitat phenological observations. This species occupies the understory of forested physiognomies with a deep groundwater table (OFC). Observed with flowers from July to August and fruits between October and December.

***Croton dissectistipulatus* Secco**
Figure 6F

Botanical family. Euphorbiaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′56.02″S, 059° 01′19.81″W; alt. 40 m; 08.II.2015; L.O. Demarchi 25 leg.; INPA 287412. • ibid.; 02.VIII.2014; L.O. Demarchi 136 leg.; INPA 268609. • ibid.; 28.VIII.2015; L.O. Demarchi 623 leg.; INPA 274250.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs in the states of Amazonas and Pará.

Identification. Shrub, 1–2 m high. Leaves alternate spiral, chartaceous, elliptic to lanceolate, apex mucronate to acuminate, base rounded to obtuse, margin crenate-glandulate. Inflorescences terminal, racemose, bisexual or unisexual; pistillate flowers 2–3 or absent at the base of the inflorescence, separated to the staminate ones by a free part. Staminate flowers: white, sepals 5, elliptic, petals 5, elliptic to lanceolate; pistillate flowers: white, calyx 5-lobate, petals absent.

Habitat and phenological observations. This species occupies the exposed soil of shrubby physiognomies with a deep groundwater table exposed to full solar radiation (OSC). Observed with flowers from July to August and fruits in February.

***Mabea uleana* Pax & K.Hoffm.**
Figure 6G

Botanical family. Euphorbiaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′49.36″S, 059° 01′14.26″W; alt. 40 m; 31.VII.2014; L.O. Demarchi 123 leg.; INPA 268599. • ibid.; 28.IV.2018; L.O. Demarchi 1146 leg.; INPA 288349. • ibid.; 10.VII.2018; L.O. Demarchi 1256 leg.; INPA 288411. • ibid.; 13.VI.2019; L.O. Demarchi 1545 leg.; INPA 288635.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs only in the state of Amazonas.

Identification. Treelet, 3–6 m high. Leaves alternate distichous, oblong-lanceolate to elliptic, apex acuminate, base obtuse to rounded, basal glands conspicuous; venation brochidodromous. Inflorescences tyrsoid, terminal. Flowers monochlamyds, pistillate címulas with 6 flowers, staminate címulas with 3 flowers, pink.

Habitat and phenological observations. This species occupies small islands of vegetation in shrubby physiognomies (OSC) and the understory of arboreal physiognomies (OAC), not tolerating direct solar radiation. Observed with flowers from April to June and fruits between June and August.

***Aldina heterophylla* Spruce ex Benth.**
Figure 6H

Botanical family. Fabaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′25.98″S, 059° 01′17.32″W; alt. 40 m; 29.IV.2018; L.O. Demarchi 1163 leg.; INPA 288358. • ibid.; 12.II.2019; L.O. Demarchi 1474 leg.; INPA 288600. • ibid.; 08.III.2019; L.O. Demarchi

1479 leg.; INPA 288604. • ibid.; 16.V.2019; L.O. Demarchi 1539 leg.; INPA 288630. • ibid.; 10.II.2020; L.O. Demarchi 1661 leg.; INPA 288731.

Geographic distribution. Amazon basin. Occurs in Brazil and Venezuela. In Brazil, this species occurs only in the state of Amazonas.

Identification. Tree or treelet, 4–25 m high. Leaves alternate spiral, compound, 1–3(–5) pinnate, leaflets coriaceous, ovate to oblong-lanceolate, apex acuminate, base rounded; venation brochidodromous, usually inconspicous. Inflorescences terminal or axillary, paniculate, with more than 70 flowers; calyx 3–4-lobate, petals 5–6, oblanceolate, white.

Habitat and phenological observations. This species occupies the canopy, distributed across all physiognomies, occupying from shrubby areas to forested areas where it can be emergent, tolerating areas with elevated or deep groundwater table. Observed with flowers from February to March and fruits between March and May.

***Dimorphandra campinarum* Ducke**
Figure 6I

Botanical family. Fabaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′04.16″S, 059° 01′06.52″W; alt. 40 m; 06.VIII.2014; L.O. Demarchi 178 leg.; INPA 268642. • ibid.; 04.IX.2018; L.O. Demarchi 1305 leg.; INPA 288455. • ibid.; 07.XI.2018; L.O. Demarchi 1418 leg.; INPA 288545. • ibid.; 14.IX.2019; L.O. Demarchi 1582 leg.; INPA 288667. • ibid.; 10.I.2020; L.O. Demarchi 1650 leg.; INPA 288721.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs in the states of Amazonas and Pará.

Identification. Treelet or tree, 3–10 m high. Leaves alternate spiral, bipinnate, subleaflets chartaceous, oblong, apex retuse to obtuse, base truncate, abaxial surface pulverulent, adaxial surface glabrous. Inflorescences paniculate-racemose, with 1–5 racemos; flowers orange, petals 5. In the area, this species is similar to *Dimorphandra pennigera*, but is distinguished by the length and color of the inflorescence (white with 12–18 cm long in *D. pennigera* and orange with up to 30 cm long in *D. campinarum*).

Habitat and phenological observations. This species occupies shrubby physiognomies exposed to full solar radiation (OSC and DSC) or the canopy of arboreal physiognomies (OAC and DAC), with elevated or deep groundwater table. Observed with flowers from August to October and fruits between October and February.

***Eperua glabriflora* (Ducke) R.S.Cowan**

Botanical family. Fabaceae

Material examined. BRAZIL – **Amazonas** • Presidente Figueiredo, Rebio Uatumã; 02°03′10″S, 059°23′40″W; 17.V.2007; L.C. Zartman 7014 leg.; INPA 227250.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs only in the state of Amazonas.

Identification. Tree, 10–20 m high. Leaves alternate distichous, paripinnate, leaflets in 2 pairs, coriaceous, ovate to elliptic, apex acute to acuminate, base rounded to obtuse, margin revolute; venation brochidodromous. Inflorescences paniculate, axillary or terminal, with 3–20 flowers; sepals ovate to elliptic, petals flabelliform, red to purple.

Habitat and phenological observations. This species occupies the canopy of forested physiognomies (OFC), with a deep groundwater table. Observed with flowers from July to August; fruits were not observed.

***Macrolobium duckeanum* R.S.Cowan**
Figure 7A

Botanical family. Fabaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′52.72″S, 059° 01′10.84″W; alt. 40 m; 14.IV.2019; L.O. Demarchi 1494 leg.; INPA 288618. • ibid.; 11.III.2020; L.O. Demarchi 1678 leg.; INPA 288746.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs in the states of Amazonas, Pará, and Roraima.

Identification. Tree, 6–14 m high. Leaves alternate distichous, paripinnate, leaflets elliptic, apex acuminate to acute, base asymmetric; venation brochidodromous. Inflorescences racemose, with 15–40 flowers; sepals 5, petals obovate, whitish-green. In the area, this species is similar to *Macrolobium punctatum* but is distinguished by the number of sepals and color of fillets (fillet red and 5 sepals in *M. duckeanum* and fillet green and 4 sepals in *M. punctatum*).

Habitat and phenological observations. This species occupies the sub-canopy of forest physiognomies with an elevated groundwater table (DFC). Observed with flowers from March to May as well as from July to September and fruits between September and January.

***Macrolobium punctatum* Spruce ex Benth.**
Figure 7B

Botanical family. Fabaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′56.02″S, 059° 01′19.81″W; alt. 40 m; 02.VIII.2014; L.O. Demarchi 168 leg.; INPA 268636. • ibid.; 31.VIII.2015; L.O. Demarchi 643 leg.; INPA 274270. • ibid.; 01.IX.2015; L.O. Demarchi 660 leg.; INPA 274287. • ibid.; 29.IX.2018; L.O. Demarchi 1363 leg.; INPA 288494. • ibid.; 02.X.2018; L.O. Demarchi 1370 leg.; INPA 288501. • ibid.; 14.IV.2019; L.O. Demarchi 1493 leg.; INPA 288617. • ibid.; 11.VIII.2019; L.O. Demarchi 1561 leg.; INPA 288648. • ibid.; 10.I.2020; L.O. Demarchi 1651 leg.; INPA 288722.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, and Venezuela. In Brazil, this species occurs in the states of Amazonas, Pará, and Roraima.

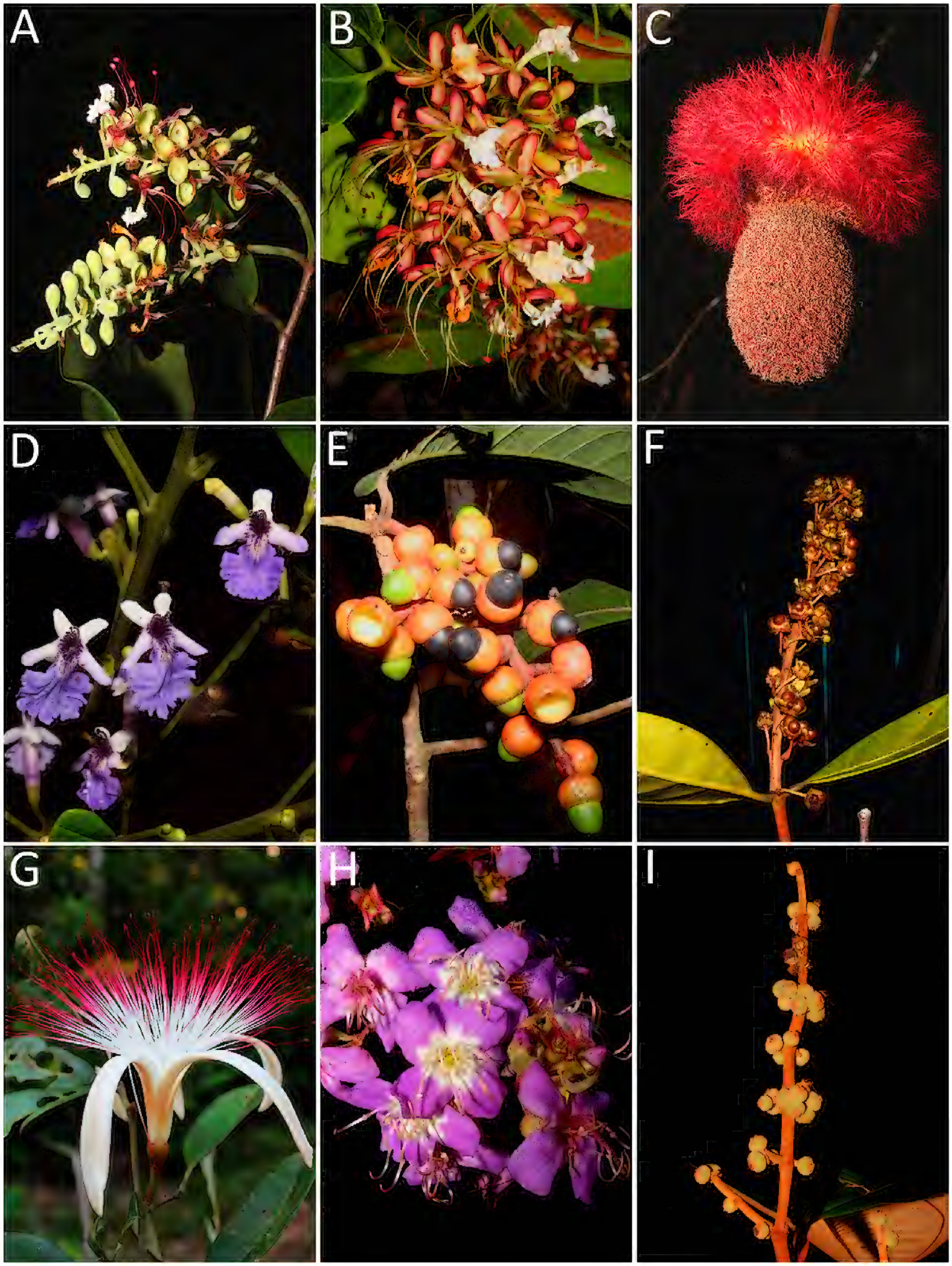

Figure 7. Some species from campinaranas of Uatumã Sustainable Development Reserve. **A.** *Macrolobium duckeanum* (Fabaceae), flowers. **B.** *Macrolobium punctatum* (Fabaceae), flowers. **C.** *Parkia igneiflora* (Fabaceae), flowers. **D.** *Vitex duckei* (Lamiaceae), flowers. **E.** *Endlicheria arenosa* (Lauraceae), immature and mature fruits. **F.** *Acmanthera minima* (Malpighiaceae), mature fruits. **G.** *Pachira faroensis* (Malvaceae), flower. **H.** *Macairea theresiae* (Melastomataceae), flowers. **I.** *Miconia subsimplex* (Melastomataceae), immature fruits.

Identification. Treelet or tree, 3–12 m high. Leaves alternate distichous, paripinnate, leaflets elliptic to lanceolate and falcate, apex acuminate to acute, base asymmetric; venation brochidodromous. Inflorescences racemose, with 10–30 flowers; sepals 4, petals obovate to suborbiculate, whitish.

Habitat and phenological observations. This species occupies shrubby and arboreal physiognomies (OSC and OAC) usually with a deep groundwater table. Observed with flowers from March to May as well as from July to October and fruits between September and February.

Parkia igneiflora **Ducke**
Figure 7C

Botanical family. Fabaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′49.36″S, 059° 01′14.26″W; alt. 40 m; 12.II.2019; L.O. Demarchi 1477 leg.; INPA 287665. • ibid.; 14.IV.2019; L.O. Demarchi 1499 leg.; INPA 287666. • ibid.; 12.XII.2019; L.O. Demarchi 1627 leg.; INPA 287667.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia Ecuador, Guyana, Peru, and Venezuela. In Brazil, this species occurs in the states of Amazonas, Pará, and Roraima.

Identification. Tree, 8–16 m high. Leaves alternate spiral, bipinnate, subleaflets with retuse apex and auricullate base. Inflorescence with clavate form, predominantly red; calyx gamosepalous, corolla gamopetalous. In the area, this species is similar to *Parkia panurensis*, but is distinguished by inflorescence peduncle length (up to 3 m in *P. igneiflora* and up to 1 m in *P. panurensis*).

Habitat and phenological observations. This species occupies the canopy of arboreal (OAC and DAC) and forested (OFC) physiognomies, where it can be emergent. Observed with flowers from January to March and fruits between March and June.

Vitex duckei **Huber**
Figure 7D

Botanical family. Lamiaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′56.02″S, 059°01′19.81″W; alt. 40 m; 28.VIII.2015; L.O. Demarchi 627 leg.; INPA 274254. • ibid.; 06.IX.2018; L.O. Demarchi 1325 leg.; INPA 288474. • ibid.; 02.X.2018; L.O. Demarchi 1372 leg.; INPA 288503. • ibid.; 11.VIII.2019; L.O. Demarchi 1557 leg.; INPA 288645.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs in the states of Acre, Amazonas, and Pará.

Identification. Treelet or tree, 3–12 m high. Leaves opposite decussate, compounds, leaflets 3, central leaflet elliptic to obovate, apex rounded, base rounded to acute; venation brochidodromous. Inflorescences with up to 7 flowers per cyme, purple.

Habitat and phenological observations. This species occupies shrubby and arboreal physiognomies (OSC and OAC) usually with a deep groundwater table. Observed with flowers from August to October and fruits between September and November.

Endlicheria arenosa **Chanderb.**
Figure 7E

Botanical family. Lauraceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′04.16″S, 059° 01′06.52″W; alt. 40 m; 31.VII.2014; L.O. Demarchi 118 leg.; INPA 268594. • ibid.; 10.VII.2018; L.O. Demarchi 1247 leg.; INPA 288402. • ibid.; 09.XII.2018; L.O. Demarchi 1438 leg.; INPA 288565. • ibid.; 10.II.2020; L.O. Demarchi 1669 leg.; INPA 288738.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, and Venezuela. In Brazil, this species occurs in the states of Amazonas, Pará, and Roraima.

Identification. Treelet or tree, 4–8 m high. Leaves alternate spiral, chartaceous to coriaceous, obovate to elliptic, apex acute to acuminate, base acute to obtuse, adaxial surface glabrous, abaxial surface puberulous; venation brochidodromous. Inflorescences subterminal to axillary, paniculate, peduncle and pedicel reddish, with >40 flowers; tepals ovate, greenish.

Habitat and phenological observations. This species occupies the understory or sub-canopy of arboreal and forested physiognomies (OAC and OFC) with a deep groundwater table. Observed with flowers from July to September and fruits between December and February.

Acmanthera minima **W.R.Anderson**
Figure 7F

Botanical family. Malpighiaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′29.86″S, 059° 01′12.97″W; alt. 40 m; 10.VII.2018; L.O. Demarchi 1249 leg.; INPA 288404. • ibid.; 02.X.2018; L.O. Demarchi 1371 leg.; INPA 288502. • ibid.; 08.III.2019; L.O. Demarchi 1485 leg.; INPA 288610. • ibid.; 10.I.2020; L.O. Demarchi 1644 leg.; INPA 288715.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs only in the state of Amazonas.

Identification. Treelet or tree, 3–10 m high. Leaves opposite decussate, elliptic, apex short-acuminate, base cuneate; venation eucamptodromous. Inflorescences sericeous; flowers in clusters of 2–3, sepals ovate to orbicular, petals 5, white.

Habitat and phenological observations. This species occupies shrubby physiognomies exposed to full solar radiation (OSC and DSC) or the sub-canopy of arboreal physiognomies (OAC and DAC), with elevated or deep groundwater table. Observed with flowers from September to November and fruits between December and February.

***Pachira faroensis* (Ducke) W.S.Alverson**
Figure 7G

Botanical family. Malvaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′29.86″S, 059° 01′12.97″W; alt. 40 m; 14.IX.2019; L.O. Demarchi 1588 leg.; INPA 288672. • ibid.; 12.XII.2019; L.O. Demarchi 1625 leg.; INPA 288705.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, and Venezuela. In Brazil, this species occurs in the states of Amazonas and Pará.

Identification. Tree, 6–15 m high. Leaves alternate spiral, compound, leaflets 3, coriaceus, elliptic to ovate, apex rounded to emarginate, base obtuse to cuneate; venation brochidodromous, 1–3 glands at the apex of petiole. Flowers solitary, white, with the distal part of stamens red, sepals 5, petals 5.

Habitat and phenological observations. This species occupies the sub-canopy of forest physiognomies with an elevated groundwater table (DFC). Observed with flowers from August to September and fruits between October and February.

***Macairea theresiae* Cogn.**
Figure 7H

Botanical family. Melastomataceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′04.16″S, 059° 01′06.52″W; alt. 40 m; 09.VII.2018; L.O. Demarchi 1233 leg.; INPA 289052.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs in the states of Amazonas, Pará, and Roraima.

Identification. Shrub or treelet, 2–4 m high. Leaves opposite decussate, obovate, apex rounded to obtuse, base cuneate; venation acrodromous. Inflorescences terminal, with 30–70 flowers, petals 4, petal apex purple to pinkish, base white. This species is highly similar to *Macairea thyrsifolia*, but is easily distinguished by the obovate leaf lamina shape and the rounded to retuse apex.

Habitat and phenological observations. This species occupies shrubby physiognomies exposed to full solar radiation (OSC and DSC) or the canopy of arboreal physiognomies (OAC and DAC), with an elevated or a deep water table. Observed with flowers from July to August and fruits between August and September.

***Miconia subsimplex* Pilg.**
Figure 7I

Botanical family. Melastomataceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′49.36″S, 059°01′14.26″W; alt. 40 m; 30.IV.2018; L.O. Demarchi 1184 leg.; INPA 289050. • ibid.; 11.VII.2019; L.O. Demarchi 1555 leg.; INPA 289058.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs only in the state of Amazonas.

Identification. Shrub or treelet, 1–2 m high. Leaves opposite decussate, elliptic, apex acuminate to caudate, base cordate to obtuse, abaxial surface ferrugineous; venation acrodromous. Inflorescences paniculate; flowers in glomerulous, petals 5. In the area, this species is similar to others *Miconia* species, but is easily distinguished by the short pedicel, with 0.2–0.5 cm long.

Habitat and phenological observations. This species occupies the understory of arboreal and forested physiognomies (OAC and OFC) with a deep groundwater table. Observed with flowers from April to June and fruits between July and September.

***Ouratea spruceana* Engl.**

Botanical family. Ochnaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′04.16″S, 059° 01′06.52″W; alt. 40 m; 31.VII.2014; L.O. Demarchi 119 leg.; INPA 268595. • ibid.; 02.VIII.2014; L.O. Demarchi 137 leg.; INPA 268610. • ibid.; 28.VIII.2015; L.O. Demarchi 620 leg.; INPA 274247. • ibid.; 10.VII.2018; L.O. Demarchi 1255 leg.; INPA 288410. • ibid.; 03.X.2018; L.O. Demarchi 1378 leg.; INPA 288509.

Geographic distribution. Amazon basin. Occurs in Brazil, Bolivia, Colombia, Guiana, and Venezuela. In Brazil, this species occurs in the states of Amazonas, Pará, Rondônia, and Roraima, with possible records in Acre, Amapá, and Mato Grosso.

Identification. Treelet or tree, 1–10 m high. Leaves alternate distichous, ovate to elliptic, apex acute, base rounded; venation eucamptodromous. Inflorescence terminal to subterminal, panicle of racemes, with 20–50 flowers; corolla yellow, petals 5.

Habitat and phenological observations. This species occupies from shrubby physiognomies (OSC), exposed to full solar radiation, to the understory of arboreal and forested physiognomies (OAC and OFC) with a deep groundwater table. Observed with flowers from July to September and fruits between September and December.

***Ternstroemia pungens* Gleason**
Figure 8A

Botanical family. Pentaphylacaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′56.02″S, 059° 01′19.81″W; alt. 40 m; 02.VIII.2014; L.O. Demarchi 172 leg.; INPA 268640. • ibid.; 28.VIII.2015; L.O. Demarchi 624 leg.; INPA 274251. • ibid.; 28.IV.2018; L.O. Demarchi 1148 leg.; INPA 288351. • ibid.; 10.I.2020; L.O. Demarchi 1646 leg.; INPA 288717.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, Guyana, and Venezuela. In Brazil, this species occurs in the states of Amazonas and Roraima.

Identification. Shrub, 1–3 m high. Leaves alternate spiral, concentrated at the apex of branches, coriaceous,

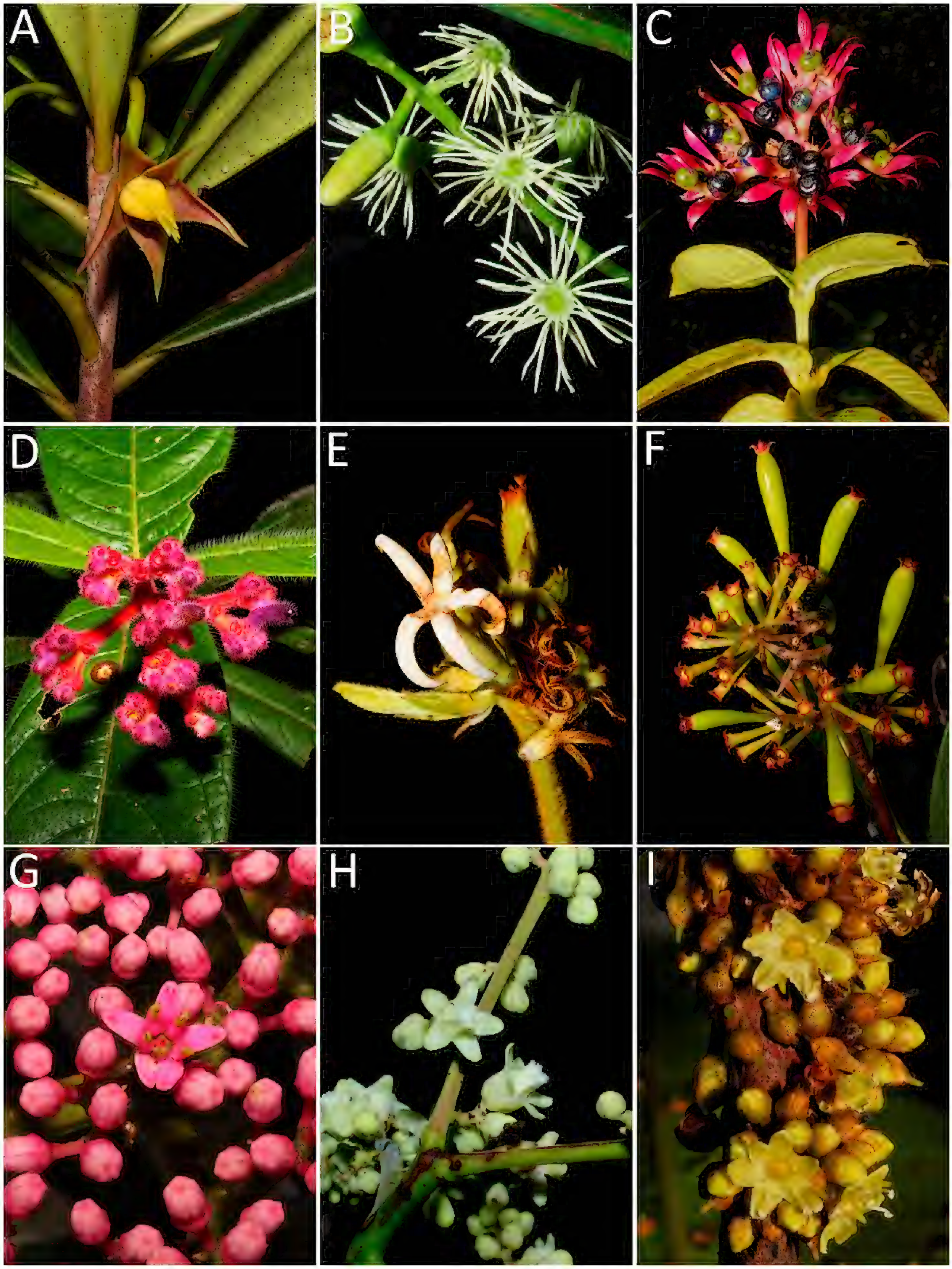

Figure 8. Some species from campinaranas of Uatumã Sustainable Development Reserve. **A.** *Ternstroemia pungens* (Pentaphylacaceae), flower. **B.** *Rhabdodendron macrophyllum* (Rhabdodendraceae), flowers. **C.** *Palicourea blakei* (Rubiaceae), immature and mature fruits. **D.** *Palicourea huberi* (Rubiaceae), buds and flowers. **E.** *Remijia hirsuta* (Rubiaceae), buds and flowers. **F.** *Remijia morilloi* (Rubiaceae), immature fruits. **G.** *Hortia longifolia* (Rutaceae), buds and flowers. **H.** *Talisia ghilleana* (Sapindaceae), buds and flowers. **I.** *Pradosia schomburgkiana* (Sapotaceae), buds and flowers.

apex obtuse to acute, base cuneate, margin revolute, black punctuations on abaxial surface; venation little conspicuous. Flowers axillary, solitary; sepals 5, brownish to reddish, petals 5. In the area, this species is similar to *Ternstroemia dentata*, but is easily distinguished by habit (shrub with many branches from the base in *T. punctata* and tree up to 15 m in *T. dentata*).

Habitat and phenological observations. This species occupies the small islands of vegetation in shrubby physiognomies (OSC) exposed to full solar radiation, and the understory of arboreal physiognomies (OAC) with elevated light intensity. Observed with flowers and fruits throughout the entire year.

***Rhabdodendron macrophyllum* (Spruce ex Benth.) Huber**

Figure 8B

Botanical family. Rhabdodendraceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′04.16″S, 059° 01′06.52″W; alt. 40 m; 20.IV.2017; L.O. Demarchi 832 leg.; INPA 277943. • ibid.; 14.IV.2019; L.O. Demarchi 1497 leg.; INPA 288621.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs in the states of Amazonas, Pará, and Roraima.

Identification. Treelet, 3–6 m high. Leaves alternate spiral, chartaceous, sessile, strictly lanceolate to oblong, apex acuminate, base cuneate; venation brochidodromous. Inflorescences racemose, with 20–50 flowers; sepals 5, petals 5, white.

Habitat and phenological observations. This species occupies the understory of forested physiognomies (OFC and DFC) with deep or elevated groundwater table. Observed with flowers from March to April and fruits between April and May.

***Sterigmapetalum plumbeum* Aymard & Cuello**

Botanical family. Rhizophoraceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′25.98″S, 059° 01′17.32″W; alt. 40 m; 06.IX.2018; L.O. Demarchi 1312 leg.; INPA 288462. • ibid.; 06.XI.2018; L.O. Demarchi 1409 leg.; INPA 288538.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs only in the state of Amazonas.

Identification. Tree, 10–25 m high. Leaves whorled, 3 per verticille, coriaceous, oblong, apex emarginated, base rounded, margin subrevolute; venation brochidodromous. Inflorescences solitary along the axils; pistillate flowers with a 5-lobate calyx, petals 5, white; staminate flowers unknown.

Habitat and phenological observations. This species occupies the canopy or may be emergent in arboreal and forested physiognomies (OAC and OFC) with a deep groundwater table. Observed with flowers from September to December and fruits between October and February.

***Palicourea blakei* (Standl. & Steyerm) Borhidi**

Figure 8C

Botanical family. Rubiaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′56.02″S, 059° 01′19.81″W; alt. 40 m; 04.XI.2018; L.O. Demarchi 1399 leg.; INPA 288528. • ibid.; 10.II.2020; L.O. Demarchi 1659 leg.; INPA 288729.

Geographic distribution. Amazon basin. Occurs in Brazil and Venezuela. In Brazil, this species occurs in the states of Amazonas and Roraima.

Identification. Shrub, 1–2 m high. Leaves opposite decussate, coriaceous, subsessile, oblong, apex acuminate, base slightly auriculate, margin revolute; venation brochidrodromous; stipules bipartite, glabrous. Inflorescences corymbose, terminal, with 30–50 flowers; vinaceous bracts; petals 5, white. In the area, this species is similar to others *Palicourea* species, but is easily distinguished by its pronounced vinaceous floral bracts.

Habitat and phenological observations. This species occupies the small islands of vegetation in shrubby physiognomies (OSC) exposed to full solar radiation, and the understory of arboreal physiognomies (OAC) with elevated light intensity. Observed with flowers from October to November and fruits between December and February.

***Palicourea huberi* Steyerm.**

Figure 8D

Botanical family. Rubiaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′49.36″S, 059° 01′14.26″W; alt. 40 m; 09.VII.2018; L.O. Demarchi 1234 leg.; INPA 288389. • ibid.; 24.XI.2020; L.O. Demarchi 1710 leg.; INPA 289088.

Geographic distribution. Amazon basin. Occurs in Brazil and Venezuela. In Brazil, this species occurs only in the state of Amazonas.

Identification. Shrub, 1–3 m high. Leaves opposite decussate, subsessile, oblong, apex acuminate, base obtuse, both surfaces hirtellous; venation brochidodromous; stipules bipartite, with hirsute trichomes. Inflorescences corymbose, terminal, with 40–70 flowers, trichomes along its entire length, pedicel red; petals 4, purple. In the area, this species is similar to others *Palicourea* species, but is easily distinguished by purple flowers and the hispid trichomes in leaves and inflorescences.

Habitat and phenological observations. This species occupies the small islands of vegetation in shrubby physiognomies (OSC), and the understory of arboreal physiognomies (OAC) with elevated light intensity. Observed with flowers from July and November, fruits were not observed.

***Remijia hirsuta* Sucre**
Figure 8E

Botanical family. Rubiaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′04.16″S, 059° 01′06.52″W; alt. 40 m; 06.IX.2018; L.O. Demarchi 1316 leg.; INPA 288466. • ibid.; 09.XII.2018; L.O. Demarchi 1426 leg.; INPA 288553. • ibid.; 10.II.2020; L.O. Demarchi 1660 leg.; INPA 288730. • ibid.; 11.III.2020; L.O. Demarchi 1679 leg.; INPA 288747.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs only in the state of Amazonas.

Identification. Treelet, 5–8 m high. Leaves opposite decussate, oblanceolate, apex acuminate, base cuneate, both surfaces hirtellous; venation brochidodromous; stipules ovate, with pubescent trichomes. Inflorescences axillary, with 20–50 flowers; sepals 5, petals 5, white. In the area, this species is similar to others *Remijia* species but is easily distinguished by the presence of hispid trichomes in leaves and inflorescences.

Habitat and phenological observations. This species occupies the understory of forested physiognomies (OFC and DFC) with deep or elevated groundwater table. Observed with flowers from February to March and fruits between April and September.

***Remijia morilloi* Steyerm.**
Figure 8F

Botanical family. Rubiaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°11′04.16″S, 059° 01′06.52″W; alt. 40 m; 06.VIII.2014; L.O. Demarchi 181 leg.; INPA 268645. • ibid.; 29.IV.2018; L.O. Demarchi 1170 leg.; INPA 288365. • ibid.; 11.I.2019; L.O. Demarchi 1467 leg.; INPA 288593. • ibid.; 10.I.2020; L.O. Demarchi 1645 leg.; INPA 288716.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, and Venezuela. In Brazil, this species occurs only in the state of Amazonas.

Identification. Shrub or treelet, 1–2 m high. Leaves opposite decussate, coriaceous, elliptic, apex rounded, base acute, margin revolute, venation brochidodromous; stipules elliptic, glabrous. Inflorescences axillary, with 30–50 flowers; sepals 5, petals 5, white-reddish. In the area, this species is similar to others *Remijia* species but is easily distinguished by the leaves coriaceous and glabrous.

Habitat and phenological observations. This species occupies the shrubby physiognomies (DSC) with an elevated groundwater table and exposed to full solar radiation. Observed with flowers in January and April and fruits between May and September.

***Hortia longifolia* Spruce ex Engl.**
Figure 8G

Botanical family. Rutaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′49.36″S, 059° 01′14.26″W; alt. 40 m; 16.V.2019; L.O. Demarchi 1540 leg.; INPA 288631.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs in the states of Amazonas, Mato Grosso, Pará, and Roraima.

Identification. Treelet or tree, 5–8 m high. Leaves alternate spiral, coriaceous, oblanceolate to strictly lanceolate, apex acute to obtuse, base attenuate, margin revolute; venation craspedodromous, secondary veins little conspicuous. Inflorescences corymbose, with >300 flowers, terminal; calyx cotiliform, 5-lobate, petals 5, pinkish.

Habitat and phenological observations. This species occupies the understory of forested physiognomies (OFC) with a deep groundwater table. Observed with flowers from April to May and fruits between June and October.

***Talisia ghilleana* Acev.-Rodr.**
Figure 8H

Botanical family. Sapindaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′56.02″S, 059° 01′19.81″W; alt. 40 m; 09.X.2015; L.O. Demarchi 685 leg.; INPA 274312. • ibid.; 02.IX.2018; L.O. Demarchi 1278 leg.; INPA 288433. • ibid.; 03.XI.2018; L.O. Demarchi 1394 leg.; INPA 288523. • ibid.; 09.XII.2018; L.O. Demarchi 1425 leg.; INPA 288552. • ibid.; 14.IX.2019; L.O. Demarchi 1579 leg.; INPA 288665. • ibid.; 24.XI.2020; L.O. Demarchi 1701 leg.; INPA 289079.

Geographic distribution. Brazilian Amazon basin. In Brazil, this species occurs only in the state of Amazonas.

Identification. Shrub or treelet, 1–4 m high. Leaves alternate spiral, paripinnate, alternate spiral, leaflets opposite to subopposite, pairs 2–3, coriaceous, elliptic to oblong, apex acuminate, base obtuse, margin revolute; venation brochidodromous. Inflorescences paniculate, with > 100 flowers; sepals 5, whitish; petals 5, whitish.

Habitat and phenological observations. This species occupies the small islands of vegetation in shrubby physiognomies (OSC) and the understory of arboreal physiognomies (OAC), with an elevated groundwater table. Observed with flowers from August to September and fruits between October and January.

***Pradosia schomburgkiana* (A.DC.) Cronquist**
Figure 8I

Botanical family. Sapotaceae

Material examined. BRAZIL – **Amazonas** • São Sebastião do Uatumã, RDS Uatumã; 02°10′49.36″S, 059°01′14.26″W; alt. 40 m; 03.XI.2018; L.O. Demarchi 1397 leg.; INPA 288526. • ibid.; 08.III.2019; L.O. Demarchi 1484 leg.; INPA 288609. • ibid.; 12.XII.2019; L.O. Demarchi 1620 leg.; INPA 288700. • ibid.; 11.III.2020; L.O. Demarchi 1681 leg.; INPA 288749. • ibid.; 24.XI.2020;

L.O. Demarchi 1716 leg.; INPA 289094.

Geographic distribution. Amazon basin. Occurs in Brazil, Colombia, Guyana, Suriname, and Venezuela. In Brazil, this species occurs in the states of Amapá, Amazonas, Pará, and Roraima.

Identification. Treelet or tree, 3–15 m high. Leaves opposite to subopposite, coriaceous, elliptic, apex rounded to acute, base rounded to obtuse, margin slightly revolute; venation brochidodromous. Inflorescences glomerular, ramiflorous, with 5–12 flowers; petals 6, greenish.

Habitat and phenological observations: This species occupies the small islands of vegetation in the shrubby physiognomies (OSC) and the canopy of the arboreal physiognomies (OAC), while in the forested areas, it occupies the sub-canopy (OFC), always with a deep groundwater table. Observed with flowers between December to January and fruits between January to May.

Discussion

Many studies point to a high number of specialized species, resulting in an endemic flora for campinarana ecosystems (Anderson 1981; Kubitzki 1989; Boubli 2002; Fine et al. 2010; Fine and Baraloto 2016; Guevara et al. 2016; Farroñay 2019; Costa et al. 2020). We found 50 species (29.9%) considered white-sand specialists, a result more expressive than 23% found by García-Villacorta et al. (2016), who analyzed a set of campinarana areas from western Amazonia based on the same species classification criteria. Farroñay (2019), compiling a set of 11 campinarana patches in the Rio Negro basin, found an even smaller proportion of specialist species, only 18% of the total. Our results corroborate that most of the species diversity found in campinarana can be attributed to plants from other habitats. However, while most species were classified as generalists, the proportion of endemic campinarana species in the USDR is high when compared to other areas with strong environmental constraints, such as várzea forests. In this habitat, Wittmann et al. (2013) found that approximately 11% of the 658 most important (abundant + frequent) tree species are endemic habitat specialists, while other 20% are floodplain specialists that can occur only sporadically and in low density in other Amazon habitats. In the Amazon non-forest vegetation of the Serra dos Carajás (cangas), a relatively small area with strong environmental constraints, Giulietti et al. (2019) found three genera and 38 endemic edaphic species, equal to 4% of the local flora.

For campinarana that is fragmented in a matrix of other habitats, such as in the USDR, the proximity can lead to a large supply of propagules from many non-white-sand specialist species from surrounding habitats (Targhetta et al. 2015), which may explain the vast proportion of generalist species found. The source of propagules from other habitats may play an important role in speciation processes within campinarana vegetation. Fine et al. (2005) demonstrated that several lineages of the tribe Protieae (mainly the genus *Protium*) that currently inhabit the campinaranas diverged from close relatives of the adjacent terra-firme forest. In the same line, Fine and Baraloto (2016) showed that the majority of dominant specialist species in campinaranas belong to clades that are not exclusive to these ecosystems, suggesting that recent ecological divergence from richer to poorer soils had occurred.

Botanical surveys in Amazonian campinaranas are usually performed with floristic inventories in plots with the area ranging between 0.3 and 6.2 ha (Table 2). Being restricted to the plot area, and in some cases depending on the inclusion criteria (DBH), a bias is included, resulting in the underestimation of species richness, for example, through the exclusion of life forms such as shrubs and treelets (Filgueiras et al. 1994). Species collected outside the plots are usually not included, with exception of the study of Vicentini (2004), and our study presented here. However, comparisons are limited due to the different methodologies used (sampled area, DBH inclusion criteria). The number of families found by us (50) was the second largest, but the number of species (167 spp.) was intermediate in comparison to other surveys in Central Amazonian campinarana (Table 2). Among the inventories that found the highest species richness, Stropp et al. (2011) recorded 290 species along the upper course of the Negro River, where campinarana is the dominant vegetation formation, unlike the other surveys listed, where it usually occurs as fragmented islands surrounded by dense terra-firme forest. In the studies of Campos (2017), carried out in the paleochannel of the Negro River (324 spp.), and Farroñay (2019), in the Rio Negro SDR (205 spp.), a possible explanation for the comparatively high number of species may be due the low inclusion criteria (dbh ≥2.5 cm and ≥1 cm, respectively) which allows sampling of small shrubs to large trees. Therefore, these methodological differences and further characteristics such as conservation status (Adeney et al. 2009), disturbance history (Prance and Schubart 1977; Ferreira et al. 2013), the geological origin (Rossetti et al. 2012, 2019), and the size of the sampled campinarana, as well as the connectivity among patches (Fine et al. 2010; Costa et al. 2020), possibly interfere in the reported species richness.

Although in some surveys more than 300 tree species were found (e.g., Campos 2017), the richness in campinarana is much lower than that reported for terra-firme forests, where on average there are 100–250 tree species per hectare (DBH ≥10 cm) (Pitman et al. 2001; Duque et al. 2017) and in some cases more than 400 tree species per hectare (Valencia et al. 1994). This pronounced difference in both species richness and composition (Gentry 1988; Stropp et al. 2011) can be explained by the extreme environmental conditions that campinarana experience throughout the year. Thus, nutrient poverty (Tiessen et al. 1994; Luizão et al. 2007; Mendonça et al. 2015), drought during dry months due to high temperatures, low water retention capacity of sandy soils (Coomes 1997; Adeney et al. 2016), and the flooding of the root system during

wet months (Richardt et al. 1975; Franco and Dezzeo 1994; Tharghetta et al. 2015) can act as strong environmental filters selecting specific taxa. These environmental filters of campinarana ecosystems are shared by other Amazonian oligotrophic ecosystems (ex: igapó and restinga), which could help to explain the 29 species considered oligotrophic habitats specialist reported in this study. However, Targhetta et al. (2015) found high dissimilarity between the campinaranas and the igapós of the USDR (less than 6 km distant from each other) with only four species shared between both ecosystems, contradicting previous studies that found high similarity between these two oligotrophic ecosystems (Kubitzki 1989; Damasco et al. 2013). But the igapó area compared in the study of Targhetta et al. (2015) is highly impacted by a hydroelectric dam (Shöngart et al. 2021), which may have influenced the results found.

In this study, Fabaceae had the highest species richness as previously reported for other campinarana sites (Table 2), a pattern also encountered for most Amazonian ecosystems (Gentry 1988). Many tree species from Fabaceae (especially the subfamilies Papilionoideae and Mimosoideae) can fix nitrogen (Sprent 2009), which may play an important role in oligotrophic ecosystems (Kreibich and Kern 2003). Other important families in this and other studies are Annonaceae, Apocynaceae, Burseraceae, Clusiaceae, Chrysobalanaceae, Lauraceae, Rubiaceae, and Sapotaceae, which are also considered representative and dominant in campinarana areas in other Amazonian countries (Fine et al. 2010; Guevara et al. 2016). These families form a group that are the richest in any campinarana area in the Amazon region (Table 2) and in many forest types, however, other families such as Lecythidaceae, Meliaceae, Moraceae, Myristicaceae, Salicaceae, Urticaceae, and Violaceae are proportionally less representative in campinaranas compared to other Amazonian vegetation types, such as terra-firme and várzea forests (Stropp et al. 2011; Wittmann et al. 2006). However, it is necessary to consider that the herbaceous and epiphytic components were not sampled; families such as Asteraceae, Cyperaceae, Orchidaceae, and Poaceae can achieve high richness in non-forest formations in the Amazon (Mota et al. 2018; Klein and Piedade 2019). Fabaceae and Rubiaceae are also the richest families in white-sand specialist species and genera, some of them, like *Pagamea*, showing a complex evolutionary history linked to the fragmented distribution of these ecosystems (Vicentini 2016).

Specialist species such as *Aldina heterophylla* (Fabaceae), *Pradosia schomburgkiana* (Sapotaceae), *Protium heptaphyllum* subsp. *ulei* (Burseraceae), *Macrolobium punctatum* (Fabaceae), *Pagamea coriacea* (Rubiaceae), *Acmanthera minima* (Malpighiaceae), and *Myrcia citrifolia* (Myrtaceae) combine elevated abundance and dominance in many campinaranas, playing an important ecological role within the plant community (Anderson et al. 1975; Ferreira 1997; Stropp et al. 2011; Targhetta et al. 2015; Campos 2017; Farronay 2019). In contrast, generalist species are often found in lower densities (García-Villacorta et al. 2016), which may be explained through the limitations for growth and reproduction of these species in this harsh environment.

Among the white-sand specialist species, USDR comprises the only non-threatened population of *Tovomita cornuta* (Clusiaceae), a rare species with only four known populations, three of them severely threatened by human activities leading to this species' status of Critically Endangered (Demarchi et al. 2021). The USDR also harbors the third known population of *Acmanthera minima*, the only species of the genus to inhabit exclusively campinarana habitats (Farroñay et al. 2019). The USDR is one of the three locations where the recently described *Clusia nascimentojuniorii* (Clusiaceae) occurs (Alencar et al. 2021). Some species, such as *Annona angustifolia* (Annonaceae), *Croton dissectistipulatus* (Euphorbiaceae), *Palicourea huberi* (Rubiaceae), *Remijia hirsuta* (Rubiaceae), *Sloanea longicaudata* (Elaeocarpaceae), and *Sterigmapetalum plumbeum* (Rhizophoraceae) are rare and poorly sampled, which does not allow for the classification of their conservational status. Two collected specimens deserve special attention: *Macrolobium* aff. *huberianum* (Fabaceae) and *Simaba* aff. *guianensis* (Simaroubaceae). After exhaustive checks on exsiccata deposited in the INPA herbaria and virtual images from herbariua worldwide, we conclude that these species may be undescribed or are taxa with unclear taxonomical delimitation.

Due to the characteristics of an oligotrophic ecosystem with extreme environmental conditions, campinaranas are considered vulnerable and with low resilience in the face of increasing disturbances associated with climate (increase of temperature and hydro-climatic extremes) (Marengo et al. 2018) and land-use changes. In the last decades, several areas have been suffering from a series of threats, such as burning (Adeney et al. 2016), selective logging (Demarchi et al. 2019), and mainly due to pressure from nearby urban centers, with the extraction of sand for building houses (Ferreira et al. 2013), which makes it essential to develop conservation strategies for these habitats. In summary, the caminaranas of USDR present a diversified flora with many specialized species to this ecosystem, with a set of rare and cryptic taxa yet to be described. The study site is a protected area under the category of a sustainable use reserve, which aims to conserve natural ecosystems in line with the subsistence of traditional populations. In this sense, our results increase the knowledge of plant communities in these important Amazonian environments, serving to support strategies for their management and conservation.

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Authors' Contributions

Conceptualization: LOD, JS, FW, MTFP. Data curation: LOD, VPK, AL, DPPA, LCM. Formal analysis: LOD. Funding acquisition: LOD, JS, MTFP, FW. Methodology: LOD, ACQ, VPK. Visualization: LOD, MJF, JC. Writing – original draft: all authors. Writing review and editing: LOD, MTFP.

Data Publishing

As our study is part of a larger project called PELD (Long-Term Ecological Research Program) financed by government agencies, all occurrence data has been deposited on the SiBBr (Sistema de Informação sobre a Biodiversidade Brasileira) platform, which is interactive with GBIF (Global Biodiversity Information Facility). To view the data deposited by the PELD MAUA project, access: https://specieslist.sibbr.gov.br/public/speciesLists

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